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THE INFLUENCE OF RED AND FAR RED LIGHT ON GROWTH AND PHOTOTROPISM OF THE AVENA SEEDLING

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(*received December 5th, 1958*)

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INTRODUCTORY REMARKS

Red light is perceived by the primary leaf of the Avena seedling, and produces or activates an unidentified substance, which we termed the red-light factor (R.L.F.). Red light also reduces the content of indole-3-acetic acid (I.A.A.) in the coleoptile, and increases the first positive phototrophic curvature induced by blue light. At low I.A.A. concentrations the R.L.F. enhances the growth rate: the curve presenting growth as a function of the I.A.A. concentration, which normally shows a single peak, is in this way transformed into a two-peaked curve. The "disposition" phenomena in phototropism are due to the interaction of the R.L.F. and I.A.A. The implications of the use of red light for the commercial growth-substance tests were studied. Far red light too reduces the I.A.A. content of the coleoptile, but it counteracts and eventually annihilates the effect of red light on the formation of the R.L.F.

CHAPTER I

INTRODUCTION AND METHODS

1. INTRODUCTION

The dark rooms in which experiments with Avena coleoptiles are made usually are lighted with orange or red light, although it is known that coleoptiles do respond in some way to these regions of the spectrum.

According to BLAAUW (1909) and to ZOLLIKOFER (1920) red light has a *phototropic* effect on the coleoptiles, but later investigators, who probably used a purer red light, could not confirm this effect.

An effect of red light on the *growth* of coleoptiles was found by VOGT as early as 1915, and this effect was confirmed by KONINGSBERGER (1922), AVERY (1937), SCHNEIDER (1941), LIVERMAN and BONNER (1953) and DE LINT (1957).

It seemed at first sight unlikely that red light would affect the rate of growth, but not the phototropic response of the coleoptiles, as a phototropic curvature is due to a difference in the rate of growth at the opposite sides of unilaterally illuminated coleoptiles. For this reason we decided to see for ourselves whether there was a phototropic response. To this end we placed coleoptiles in a spectrum, and observed that phototropic curvatures were actually formed in the red part of the spectrum too. On closer examination this phenomenon appeared to be due to scattered blue light, but a rough estimate of the intensity of the scattered light showed that the latter could not have caused a curvature of the size that was actually obtained.

This suggested that the red light itself did not induce a curvature, but that it influences the phototropic response to blue light. This possibility was investigated in a series of experiments described in this paper.

2. MATERIAL AND GENERAL METHODS

The experiments were made with seedlings of *Avena sativa* c.v. "*Siegeshafer*". Unhusked grains were thoroughly wetted by shaking them in tap water, and put to germinate on moistened filterpaper in a closed petri dish; the latter was placed under an orange lamp at a temperature of 22° C. After 24 hours the grains were planted in moist vermiculite or in glass holders in a dark room which was kept at the same temperature of 22° C and at a relative humidity of 75 %. When the plants were 88 hours old, they were used for the experiments.

All solutions of indole-3-acetic acid (I.A.A. or heteroauxin) were made with tap water containing 750 mg/l KCl and 0.2 ml/l glacial acetic acid.

The orange light was obtained from incandescent lamps (220 Volt, 20 Watt) by the use of Schott OG 2 filters. Monochromatic light was produced by an incandescent lamp (12 Volt, 100 Watt) in combination with a set of lenses in order to get a parallel beam and with an interference filter made by BALZER (Liechtenstein), of which the tolerance was 0.5 %. Monochromatic light of higher intensity was obtained by the use of an approximatively parallel beam from a more powerful incandescent lamp (60 Volt, 3000 Watt) in combination with a similar interference filter. The light intensity was measured either by means of a thermopile after MOLL (Kipp, Delft) or with a barrier-layer cell from Tungsram. The sensitivity of the thermopile was not sufficient for the measurement of the lower light intensities. Therefore these measurements were carried out by means of the barrier-layer cell which was calibrated for each wave length by means of the thermopile. As an indicator instrument a ZERNIKE galvanometer (Kipp, Delft) was used. In view of the large variability of the plant material no greater precision than 10 % was aimed at.

Whenever an exact wave length is mentioned, transmission spectra obtained with the interference filters are meant; Fig. 1 is a representative example of such a spectrum. The half-peak width in each case is ± 8 mμ. A summary of the light sources and filters that were used and of the light intensities that were obtained are given in the table on page 4. The figures given in the tables on experiments are the mean values of the curvatures, or of the rate of growth, measured in a number of coleoptiles. The variation is expressed as the standard error of the mean:

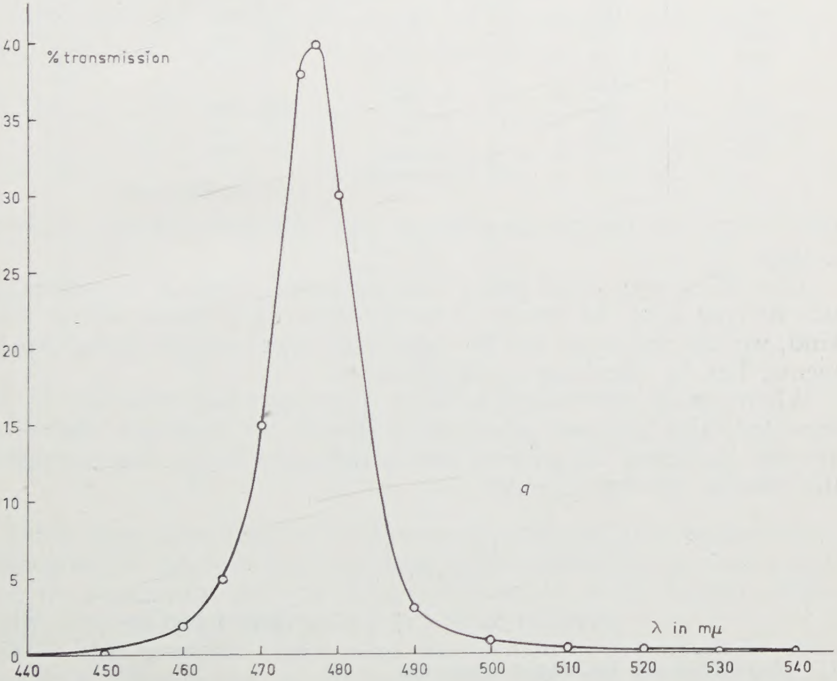

Fig. 1. Example of a transmission spectrum obtained by means of an interference filter.

$$SE_M = \pm\sqrt{\frac{\sum (v-m)^2}{n\,(n-1)}}$$

n = the number of coleoptiles (always mentioned between brackets)
$\sum (v-m)^2$ = the sum of the squared deviations from the mean.

Sometimes the results are given in the form of a graph. The figures

Light	Light source: incandescent bulb		Filter		Light intensity in ergs/cm² sec.
colour, resp. wave length	energy in Watts	tension in Volts	kind	transmission maximum at λ	
Orange	20	220	Schott	> 550 mμ	400
Green	75	220	Schott	520–620 mμ	400
λ in mμ					
480	100	12	int. f.	477 mμ	0.5
	3000	60	int. f.		20
560	100	12	int. f.	562 mμ	0.6
	3000	60	int. f.		20
580	100	12	int. f.	586 mμ	0.5
600	100	12	int. f.	595 mμ	0.9
620	100	12	int. f.	614 mμ	1.4
640	100	12	int. f.	644 mμ	1.9
660	100	12	int. f.	657 mμ	2.1
	3000	60	int. f.		70
680	100	12	int. f.	682 mμ	2.9
700	100	12	int. f.	702 mμ	2.3
740	100	12	int. f.	741 mμ	2.5
	3000	12	int. f.		50

from which the graphs were drawn, are, moreover, always given in a table.

The following general policy was pursued: whenever a conclusion was derived from the results of two or three experiments of the same kind, we did not try to test its validity by repeating the same experiments, but by checking its implications.

Where small differences between experimental series are to be expected, this method presumably should be preferred above an attempt to reduce the error of such a difference by greatly increasing the number of experiments.

CHAPTER II

INFLUENCE OF ORANGE LIGHT

1. Experiments on phototropism

In the first place we investigated whether orange light influences the size of the curvature induced by unilateral illumination with blue light.

Method

Germinated seeds were placed vertically, with the embryo pointing downwards, in vermiculite, 8 in a row. The plants were kept in absolute darkness, except for a period of ten minutes 46 hours after they had been placed in the vermiculite, at which time they were watered.

When the plants were 88 hours old, each series of 8 plants was transferred, also in absolute darkness, to the illumination apparatus. The coleoptiles were exposed with their narrow side to an unilateral illumination with different amounts of light of $\lambda = 480$ mμ, either at once or after a previous illumination with light of a different wave length.

$1\frac{1}{2}$ hours after the illumination with light of $\lambda = 480$ mμ the coleoptiles were severed from the seeds, placed on photographic paper, and shadowgraphed. The curvatures were measured by means of a protractor.

EXPERIMENTS

Coleoptiles, whether pre-illuminated from above with 36×10^4 ergs/cm^2 orange light or not pre-illuminated, were illuminated unilaterally with progressively larger amounts of light of $\lambda = 480$ mμ, which all induced a first positive curvature.

In Table I the curvatures measured in two experiments are given. The results of experiment I have been plotted in Fig. 2.

TABLE I

Exp. No.	Light quantity $\lambda = 480$ mμ in ergs/cm^2	Not pre-illuminated curvature in degrees	Pre-illuminated with 36.10^4 ergs/cm^2 orange light curvature in degrees
I	1	6.3 ± 0.5 (6)	4.7 ± 0.8 (8)
	2	10.4 ± 1.6 (8)	9.0 ± 0.8 (9)
	3	12.8 ± 1.1 (8)	9.0 ± 0.9 (7)
	5	13.0 ± 1.2 (6)	16.4 ± 1.4 (8)
	20	12.0 ± 1.1 (10)	21.1 ± 1.0 (7)
	120	8.5 ± 0.3 (12)	22.9 ± 1.0 (8)
II	1	8.0 ± 2.5 (4)	7.7 ± 1.0 (6)
	5	14.0 ± 1.0 (9)	21.2 ± 1.0 (6)
	10	14.0 ± 0.9 (7)	23.2 ± 3.2 (5)
	20	13.7 ± 1.0 (7)	23.5 ± 3.5 (4)
	30	12.5 ± 1.4 (8)	19.4 ± 1.8 (5)

From these experiments it appears that orange light undoubtedly influences the phototropic curvature of the coleoptiles in such a way that the maximum value is enhanced from 14 to 23 degrees, which really seemed surprising.

Now the question arises why no curvatures are observed after unilateral illumination of the coleoptiles with red or orange light. This might be explained by the aid of various suppositions.

a. The coleoptile contains but a very small amount of the pigment that absorbs the orange light. Consequently with unilateral illumination the light-intensity gradient in the coleoptile is not considerable, and light saturation at the light and the shade side is already reached when but relatively small amounts of orange light are administered. In that case curvatures could be expected only after illumination with very low intensities of orange light. It appeared however that under this condition too no curvatures are obtained. This supposition therefore may be discarded.

b. Orange light induces the formation of more blue-absorbing pigment with as a consequence a steepening of the light-intensity gradient in the coleoptiles when they are illuminated afterwards unilaterally with blue light. The reduction of the first positive phototropic curvature after irradiation with increasing light quantities admittedly may be due to the fact that the growth at the shade side too begins to react upon the illumination. The presence of more blue-absorbing pigment therefore would entail that a larger amount of blue light would be needed to produce this reaction of the shade side. In this case orange light should have no influence if it was applied after the illumination with blue light. In Table II the curvatures are recorded of coleoptiles which were irradiated with orange light either before or after the illumination with blue light. It appears that there is no difference in the size of the curvatures.

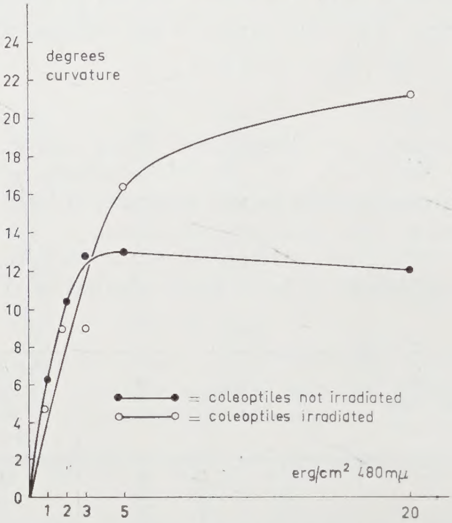

Fig. 2. The phototropic curvature of coleoptiles: ● not pre-irradiated, ○ pre-irradiated with orange light.

TABLE II

Unilateral illumination	Curvature in degrees
20 ergs/cm² λ = 480 mμ	14.7 ± 1.3 (10)
20 ergs/cm² λ = 480 mμ, followed by 36 × 10⁴ ergs/cm² orange light from above	27.9 ± 1.1 (14)
20 ergs/cm² λ = 480 mμ, preceded by 36 × 10⁴ ergs/cm² orange light from above	28.5 ± 1.4 (13)

Moreover, it could be shown that pre-illumination with orange light from the future shade side of the coleoptile has the same effect as pre-illumination from the future light side (Table III).

TABLE III

Unilateral illumination with 20 ergs/cm² λ = 480 mμ after

unilateral pre-illumination	curvature in degrees
none	10.7 ± 0.9 (9)
9.6 × 10⁴ ergs/cm² orange light from the future light side	22.7 ± 2.0 (7)
9.6 × 10⁴ ergs/cm² orange light from the future shade side	22.7 ± 0.8 (9)

For these reasons we consider it unlikely that orange light would induce the formation of a blue-absorbing pigment.

c. A third way to explain the effect of orange light was derived from the results of a number of experiments on the place where the orange light is perceived.

It could be demonstrated that particularly the tip of the seedling is sensitive to orange light.

2. LOCATION OF THE SENSITIVITY TO ORANGE LIGHT

METHOD

In absolute darkness the tips of the coleoptiles were supplied with tin foil caps of 4 mm length, the very same that ARISZ had used in 1914 to study the influence of illumination on the base part of the coleoptile.

Then the coleoptiles were supplied with a dose of orange light, whereupon the caps were removed in darkness. Next the coleoptiles were unilaterally illuminated with light of $\lambda = 480$ mμ (20 ergs/cm^2) in order to obtain a first positive curvature as large as possible.

EXPERIMENTS

TABLE IV

Unilateral illumination with 20 ergs/cm^2 $\lambda = 480$ mμ after

Exp. Nr.	Pre-illumination	Curvature in degrees
I	none	10.7 ± 0.9 (9)
	9.6×10^4 ergs/cm^2 orange light, without caps	22.7 ± 2.0 (7)
	9.6×10^4 ergs/cm^2 orange light, with caps	9.7 ± 1.9 (7)
	28.8×10^5 ergs/cm^2 orange light, with caps	15.5 ± 2.7 (6)
II	none	13.0 ± 1.7 (7)
	24.6×10^4 ergs/cm^2 orange light, without caps	19.0 ± 1.4 (12)
	24.6×10^4 ergs/cm^2 orange light, with caps	11.0 ± 1.4 (11)

From Table IV in which the resulting curvatures are recorded, it is clear that orange light has no influence at all or but a very slight influence if the upper most 4 mm of the seedling are screened from it.

Since the possibilities *a* and *b* had to be rejected, one cannot arrive at another conclusion than that it is not the tip of the coleoptile, but the tip of the primary leaf that responds to the orange light.

It was technically impossible to confirm this conclusion by removing the primary leaf in darkness and by studying the reactions to orange light of the remainder of the plant.

Therefore we passed on to the application of the standard Avena test, because it could be shown that orange light influences the curvatures in the standard Avena test as well.

3. THE EFFECT OF ORANGE LIGHT ON THE STANDARD AVENA TEST

METHOD

Avena seedlings were cultivated in glass holders as described in chapter I. They were illuminated with orange light while germinating on filter paper and also during the first 24 hours after they had been put in the glass holders. From the 48th hour on till the test they were growing in absolute darkness, except at the 72nd hour when a selection was carried out in orange light. When the plants were 88 hours old, the relative humidity of the conditioned room was raised from 75 % to 96 %.

The racks with their 12 plants remained in absolute darkness till the very moment of decapitation. With part of the plants the first decapitation was performed in darkness; the remainder were decapitated in orange light.

The coleoptiles were decapitated for a second time after an sojourn of 2 hours in green light ($\lambda = 560$ mμ). The primary leaf was loosened after the second decapitation because this manipulation could not be performed in darkness.

Two hours after the second decapitation agar blocks of 3.6 mm^3 soaked in a solution of I.A.A., were placed unilaterally upon the stumps. After another two hours shadowgraphs of the test plants were taken. Between these actions the plants were kept in the dark.

EXPERIMENTS

The curvature of plants which had been decapitated in orange light was compared with the curvature of plants which had been gropingly decapitated in darkness. After the first decapitation all manipulations were performed in green light. In Table V the curvatures produced by agar blocks containing various amounts of I.A.A. are presented.

TABLE V

I.A.A. concentration in g/ml	Curvature in degrees Decapitation in the dark		Decapitation in orange light	
$0.25 \cdot 10^{-7}$	9.0 ± 0.5	(11)	7.8 ± 0.9	(9)
$0.50 \cdot 10^{-7}$	12.5 ± 0.5	(22)	11.4 ± 0.9	(19)
$0.75 \cdot 10^{-7}$	17.6 ± 1.0	(12)	15.2 ± 1.0	(9)
$1.00 \cdot 10^{-7}$	21.2 ± 2.4	(9)	13.5 ± 0.5	(11)
$1.25 \cdot 10^{-7}$	14.1 ± 0.7	(23)	14.7 ± 0.5	(22)
$2.00 \cdot 10^{-7}$	14.9 ± 1.5	(10)	12.1 ± 1.2	(12)

It appears that orange light applied during the first decapitation reduces the size of the maximum curvature (at a concentration of I.A.A. of 10^{-7} g/ml) from about 21° to about 14°. This effect of orange light is unexplained, but it seemed a suitable means to check the supposed perception of the orange light by the primary leaf.

To that purpose the first decapitation was carried out with part of the plants in orange light and with the control plants in darkness. In case the plants were decapitated in orange light, the primary leaf was loosened either immediately after the first decapitation or after the second.

In the first case the primary leaf was left intact only during two or three minutes after it had been exposed to the orange light, in the second case it remained intact for two hours. Further manipulations were carried out in green light of $\lambda = 560$ mμ.

The solution of 10^{-7} g/ml I.A.A. was the only one that was used in these tests, because in preliminary experiments the effect of orange light proved to be largest at this concentration.

It appears (Table VI) that orange light reduces the curvature only when the primary leaf is left intact during some time after the irradiation. It therefore was concluded that indeed it is the primary leaf which perceives the orange light.

TABLE VI

First decapitation	Primary leaf removed	Curvature in degrees
in the dark	after 2nd decapitation	15.7 ± 0.7 (33)
in orange light	after 1st decapitation	16.6 ± 0.6 (24)
in orange light	after 2nd decapitation	12.9 ± 0.4 (32)

The experiments on the influence exercised by orange light on coleoptiles with screened tip showed that it should be particularly the tip of the primary leaf that responds to the orange light.This was checked as follows.

At the first decapitation, performed either in orange light or in darkness, the tip of the seedling was removed as a whole, whereas in the control series the tip of the coleoptile was taken away but the tip of the primary leaf was left intact. At the second decapitation in all series the primary leaf was loosened. Except the first decapitation all manipulations were carried out in green light of $\lambda = 560$ mμ. A solution of 10^{-7} g/ml I.A.A. was used as a test solution.

From Table VII it is obvious that orange light reduces the curvature only if the tip of the primary leaf is left intact during some time after the irradiation.

TABLE VII

First decapitation	Tip of the primary leaf	Curvature in degrees
in the dark	intact	16.1 ± 0.7 (35)
in the dark	removed	17.1 ± 0.7 (33)
in orange light	intact	12.8 ± 0.6 (35)
in orange light	removed	15.9 ± 0.6 (33)

4. CONCLUSION AND DISCUSSION

From the preceding series of experiments it is clear that orange light influences the phototropic reactions and the reaction on I.A.A. of Avena coleoptiles via the tip of the primary leaf. That the tip of a leaf may play a special part, did come to our knowledge from a publication of SHARMAN (1942), who observed that in *Zea* leaves elongation as well as the differentiation of the tissues start at the leaf tip and from a paper of ROBERTS (1951), who stated that in wheat the tip of the first leaf has a larger chlorophyll content than the rest of the leaf.

We did not occupy ourselves with the reactions of the primary leaf to orange light, but we confined our investigations to the indirect consequences of such an illumination appearing in the behaviour of the coleoptile. By what means the primary leaf influences the coleoptile, will not be considered. Maybe some substance is formed by the leaf and transported to the coleoptile, maybe the growth of the primary leaf is influenced by the orange light in such a manner that the substances which are transported upwards from the grain, are distributed differently between coleoptile and primary leaf.

5. Summary

Orange light increases in Avena coleoptiles the maximum size of the first positive curvature induced by unilateral illumination with blue light. The orange light is probably perceived by the tip of the primary leaf. The standard Avena test too is influenced by orange light, which reduces the curvatures caused by the unilateral application of I.A.A. (10^{-7} g/ml). In this case too the tip of the primary leaf proved to be the place of perception of the orange light.

CHAPTER III

DETERMINATION OF THE MOST EFFECTIVE WAVE LENGTH

An action spectrum for the influence which light of the longer wave lenghts exercises on the Avena coleoptile is not known. An action spectrum for the inhibition of growth in the mesocotyl was obtained by Weintraub and Price (1947) as well as by Goodwin and Owens (1948). However, since it is uncertain whether the same mechanism is responsible for the way in which the coleoptile and the mesocotyl react to wave lengths larger than $\lambda = 600$ mμ, it is not justified to assume that the action spectrum will be the same for both reactions.

We investigated which wave length was most effective in influencing the phototropic curvature of Avena coleoptiles in the way described in chapter II. The variability of the plant material however was so large that it proved impossible to determine an approximatively accurate action spectrum.

Coleoptiles were cultivated as described in chapter II under the heading "phototropism". They were pre-illuminated unilaterally with light of various wave lengths (in chapter II it was shown that the effect of pre-illumination is independent of the direction from which it is applied). Immediately after being pre-illuminated they were irradiated one-sidedly with 20 ergs/cm² $\lambda = 480$ mμ, i.e. with the amount of light which gives a maximum positive curvature.

The results of these experiments are summarized in Table VIII. The values given for the curvatures are the mean of six experiments.

TABLE VIII

Pre-illuminated with	Phototropic curvature in degrees	
-----	13.1 ± 0.4	(109)
30–70 ergs/cm² $\lambda = 560$ mμ	13.4 ± 0.6	(51)
30–70 ergs/cm² $\lambda = 580$ mμ	14.9 ± 0.5	(64)
30–70 ergs/cm² $\lambda = 600$ mμ	14.1 ± 0.7	(36)
30–70 ergs/cm² $\lambda = 620$ mμ	14.3 ± 0.6	(51)
30–70 ergs/cm² $\lambda = 640$ mμ	13.6 ± 0.6	(46)
30–70 ergs/cm² $\lambda = 660$ mμ	17.8 ± 0.9	(36)
30–70 ergs/cm² $\lambda = 680$ mμ	17.1 ± 1.3	(31)
30–70 ergs/cm² $\lambda = 700$ mμ	12.6 ± 0.9	(36)

In each experiment the influence of a complete series of wave lengths was investigated in order to avoid difficulties caused by the daily variability of the plants.

It appears that light of the wave lengths $\lambda = 660$ mμ and 680 mμ was most effective in enhancing the maximum size of the first positive curvature. So it was decided to continue our experiments with light of $\lambda = 660$ mμ.

The joint effect of the variability shown by the response to red light and the variability of the phototropic reaction to the blue light, however, makes it impossible to arrive at a complete action spectrum by means of these experiments. To this purpose a process more directly dependent on the red light should be used as indicator, preferably the increase in length of the coleoptiles. A sensitive auxanometer (KONINGSBERGER, 1922) should be used to this end.

SUMMARY

In this chapter it is shown that with the Avena coleoptiles light of the wave lengths $\lambda = 660$ and 680 mμ is most effective in enhancing the maximum size of the first positive phototropic curvature caused by blue light.

CHAPTER IV

THE REACTION OF THE AVENA COLEOPTILE TO LIGHT OF $\lambda = 660$ mμ IN CONNECTION WITH ITS GROWTH-SUBSTANCE METABOLISM

1. DATA FROM THE LITERATURE

Several authors have tried to connect the reactions of plants to red light with their growth-substance metabolism. HILLMAN and GALSTON (1957) summarize the literature on this subject, but in view of the fact that too different materials were treated in too different ways, they consider any attempt to discuss their own work in terms of the reports cited by them as sheer speculation. We subscribe to the view of these authors.

LIVERMAN and BONNER (1953) are the only workers to choose the Avena coleoptile as experimental object. According to their results red and far red light influence the reactions of isolated coleoptile cylinders to heteroauxin. In the hope that the influence of red light on the phototropic behaviour of the coleoptiles might be explained by the findings of these authors, we tried to reproduce their results; however, without success. Probably the discrepancy between their results and ours should be attributed to the use of different light quantities. In our experiments the coleoptile cylinders were illuminated with 700 ergs/cm^2 $\lambda = 660$ mμ, whereas in the experiments of LIVERMAN and BONNER a much larger quantity of light was applied during 30 minutes (filtered light obtained from 2 daylight fluorescent tubes was used). Obviously their experiments cannot be compared to ours. Still the possibility existed that illumination with light of $\lambda = 660$ mμ influences the heteroauxin content of the coleoptile.

To avoid the difficulties and problems with which extraction and quantitative determination of I.A.A. are beset, the I.A.A. content of the coleoptiles was estimated by means of the cylinder test.

Maximal growth of coleoptile cylinders derived from illuminated plants should occur at an I.A.A. concentration of the medium which differs from the I.A.A. concentration inducing maximum growth in cylinders cut from non-illuminated plants.

2. CYLINDER TEST (STRAIGHT-GROWTH TEST)

METHOD

The coleoptiles were cultivated in vermiculite as described in chapter I. When the plants were 88 hours old, part of them was illuminated with 700 ergs/cm² $\lambda = 660$ mμ, and part was kept in darkness. 1½ hours after the illumination the coleoptiles were placed in a coleoptile microtome after VAN DER WEY, and 3 mm tips were taken off and rejected. The next 3 mm sections were used in the experiments. Twelve sections were floated on the surface of 10 ml of a solution of I.A.A. in a buffer of 0.0025 m K-maleate adjusted with KOH on a pH of 4.5 and containing 3 % sucrose. All manipulations were carried out in green light of $\lambda = 560$ mμ. After three hours the length of the sections was measured under a microscope.

EXPERIMENTS

A series of experiments was carried out in each of which the influence of a range of I.A.A. concentrations was tested on sections of irradiated and non-irradiated plants. In Table IX the final lengths of the sections are shown in units of the eye-piece micrometer (50.9 units = 3 mm).

Experiments I and II are examples of experiments in which the optimum concentration of I.A.A. was estimated. In experiment I the optimum I.A.A. concentration seemed to be 10^{-8} g/ml for the growth of sections of irradiated plants, against 2.10^{-8} g/ml for the growth of sections of non-irradiated ones. In experiment II however sections of irradiated plants appear to show two growth maxima at different I.A.A. concentrations, whereas sections of non-irradiated plants appear to show only one growth maximum. This phenomenon was confirmed in experiments in which lower I.A.A. concentrations were used. Two examples are presented in Table IX, III and IV and in Fig. 3.

DISCUSSION

Pre-illumination of intact plants with light of $\lambda = 660$ mμ undoubtedly influences the way in which coleoptile sections subsequently react on I.A.A. The essential difference between the concentration-growth curves of coleoptile sections obtained from irradiated and non-irradiated plants may be seen in two fundamentally different ways.

1. The concentration-growth curve of irradiated coleoptile sections shows two maxima, whereas the curve of non-irradiated sections

TABLE IX

Illumination with 700 ergs/cm² $\lambda = 660$ mμ. Final length of sections

Concentr. of I.A.A. in g/ml	I Plants		II Plants	
	illuminated	not illuminated	illuminated	not illuminated
0	52.0 ± 0.7	53.0 ± 0.4	48.5 ± 0.5	51.4 ± 0.4
6.10^{-9}	—	—	54.4 ± 0.3	53.4 ± 0.2
1.10^{-8}	54.1 ± 0.3	51.1 ± 0.2	50.6 ± 0.2	53.2 ± 0.3
2.10^{-8}	53.7 ± 0.4	54.9 ± 0.3	—	—
6.10^{-8}	—	—	50.1 ± 0.4	55.1 ± 0.3
1.10^{-7}	53.3 ± 0.5	53.3 ± 0.3	52.1 ± 0.3	55.1 ± 0.5
1.10^{-6}	52.8 ± 0.5	52.5 ± 0.5	54.3 ± 0.5	55.8 ± 0.6
1.10^{-5}	51.2 ± 0.3	51.0 ± 0.2	—	—
	III		IV	
0	48.8 ± 0.4	51.4 ± 0.6	50.6 ± 0.1	52.4 ± 0.2
1.10^{-10}	52.5 ± 0.3	50.0 ± 0.3	51.2 ± 0.3	51.9 ± 0.3
1.10^{-9}	51.9 ± 0.4	50.2 ± 0.2	52.6 ± 0.1	52.6 ± 0.3
3.10^{-9}	55.8 ± 0.5	50.5 ± 0.2	54.1 ± 0.3	51.9 ± 0.2
1.10^{-8}	50.5 ± 0.3	53.5 ± 0.3	52.3 ± 0.2	53.0 ± 0.2
3.10^{-8}	54.3 ± 0.3	55.4 ± 0.5	55.5 ± 0.3	54.7 ± 0.3
1.10^{-7}	55.8 ± 0.3	55.9 ± 0.2	56.5 ± 0.5	55.8 ± 0.5

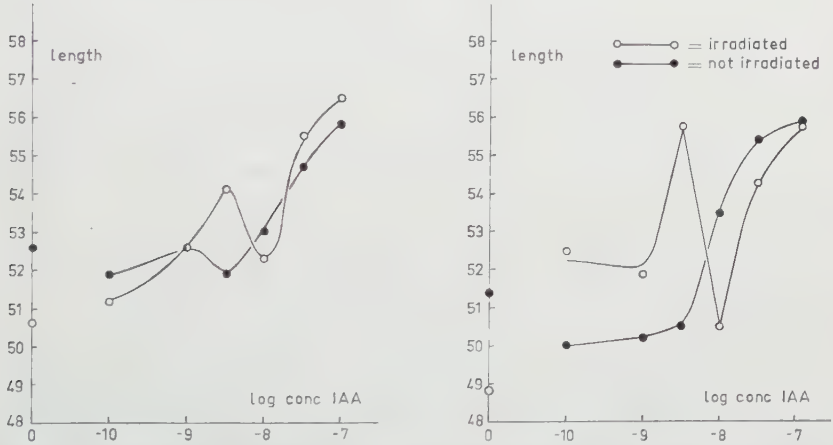

Fig. 3. Final length reached in I.A.A. solutions by coleoptile sections cut from non-irradiated seedlings and from seedlings irradiated with light of $\lambda = 660$ mμ.

shows only one. In this case no attention has been paid to the phenomenon that very low concentrations of I.A.A. inhibit the growth of non-irradiated sections. This phenomenon has also been reported by Barlow, Hancock and Lacey (1957) as appearing in tests that were carried out with sections of wheat coleoptiles. The authors attribute this to the displacement of an endogenous auxin by I.A.A.

2. The two concentration-growth curves are essentially equal. Both show two maxima, but whereas the first maximum of the irradiated sections is to be found at an I.A.A. concentration of about

$3.10\ ^{9}$ g/ml, the first maximum for the non-irradiated sections appears at an I.A.A. concentration 0. So in this case the curve for the irradiated sections is regarded as compressed and shifted to higher I.A.A.-concentrations as compared to the curve for the non-irradiated sections.

In both cases we pass over the fact that sometimes the sections in the blank buffer solution did not grow, but did shrink on the contrary.

It was investigated whether in the curvature test too the concentration-growth curve would show two maxima; in this way we hoped to exclude the possibility that our conclusion was due to bias.

3. THE CURVATURE TEST

METHOD

The test plants were cultivated as described in chapter II under the heading "Standard Avena-test".

When the plants were 88 hours old, part of them were illuminated with 70 ergs/cm² $\lambda = 660$ mμ. The others were kept in darkness. During 1½ hours after the irradiation the plants remained in darkness, whereafter the first decapitation was carried out in orange light. Immediately after the decapitation the primary leaf was loosened to prevent the orange light from influencing the reactions of the coleoptile (compare chapter II), and an agar block was applied unilaterally. Our intention was to investigate whether irradiation with light of $\lambda = 660$ mμ would induce two maxima of curvature. So in order to prevent the coleoptile from consuming the substance that possibly brings about the first maximum (at a low I.A.A.concentration) I.A.A. was applied immediately after the first decapitation, and the second decapitation was omitted. Each concentration of I.A.A. was tested on six coleoptiles.

EXPERIMENTS

The size of the curvatures as they appeared in three different experiments two hours after the application of I.A.A., are given in Table X. In Fig. 4 the results of experiment II are plotted.

TABLE X

Curvature in the Avena test after illumination with 700 ergs/cm² $\lambda = 660$ mμ

Concent. of I.A.A. in g/ml	I plants		II plants		III plants	
	illumin.	not illumin.	illumin.	not illumin.	illumin.	not illumin.
$0.3\ 10^{-7}$	—	—	6 ± 1	6 ± 2	8 ± 1	10 ± 2
$0.4\ 10^{-7}$	—	—	11 ± 1	7 ± 2	9 ± 1	11 ± 2
$0.5\ 10^{-7}$	13 ± 2	13 ± 2	17 ± 2	11 ± 2	16 ± 2	13 ± 1
$0.6\ 10^{-7}$	15 ± 2	15 ± 2	18 ± 2	13 ± 2	18 ± 2	11 ± 2
$0.7\ 10^{-7}$	24 ± 1	18 ± 1	16 ± 2	15 ± 3	20 ± 2	14 ± 2
$0.8\ 10^{-7}$	23 ± 2	17 ± 2	18 ± 2	18 ± 2	18 ± 3	17 ± 1
$0.9\ 10^{-7}$	19 ± 3	24 ± 2	22 ± 1	21 ± 2	20 ± 1	24 ± 2
$1.0\ 10^{-7}$	25 ± 3	27 ± 2	21 ± 2	21 ± 1	19 ± 3	24 ± 2
$2.0\ 10^{-7}$	26 ± 2	30 ± 2	27 ± 3	23 ± 1	27 ± 3	25 ± 1
$4.0\ 10^{-7}$	30 ± 3	32 ± 1	30 ± 2	23 ± 4	30 ± 5	28 ± 1
$6.0\ 10^{-7}$	33 ± 3	33 ± 1				

DISCUSSION

On condition that each experiment is considered by itself, the curvature-concentration curve shows one maximum for the non-irradiated plants, two for the irradiated ones. The first maximum of the irradiated plants appears in the experiments I and II as a more or less pronounced peak, in experiment III as a platform. In each of the three experiments the curvature of the irradiated plants at an I.A.A. concentration of 0.6 or 0.7 $\times 10^{-7}$ g/ml is significantly larger than the curvature of the non-irradiated ones. Presumably it is not admissible to average the results of the three experiments, the variability shown by the plants from day to day being too large.

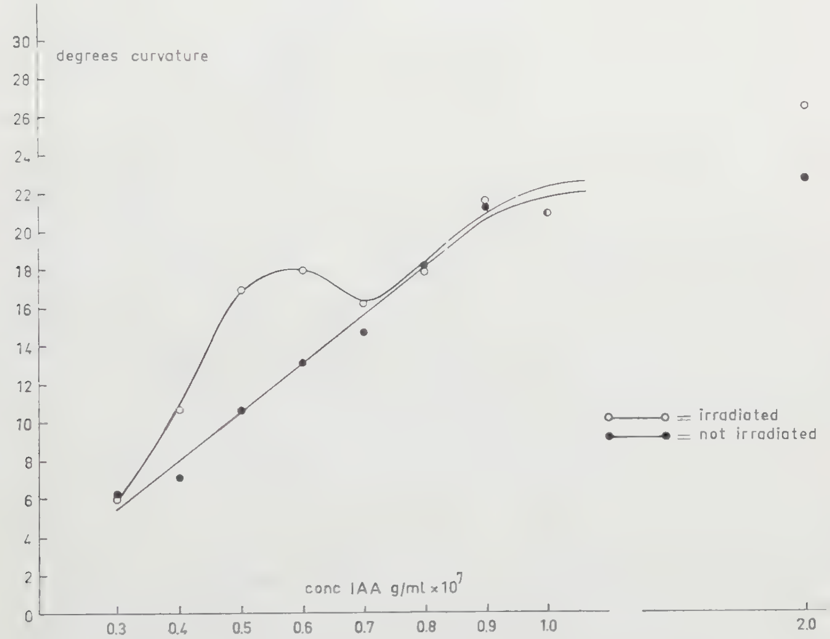

Fig. 4. Curvature reached in the curvature test by non-irradiated coleoptiles and by coleoptiles irradiated with light of $\lambda = 660$ mμ.

To counter the argument that the differences in curvature observed at the same I.A.A. concentration might be due to the variability of the plants and not to the irradiation, the curvatures of three series of non-irradiated plants were studied. They were treated in exactly the same way as the irradiated and non-irradiated series in the above-mentioned experiments. Agar blocks soaked in the same I.A.A. solution were applied to each series. Table XI shows the resulting curvatures. At the same I.A.A. concentration the differences in curvature observed between the plants of series a, b, and c are not nearly so large as those observed between irradiated and non-irradiated plants.

TABLE XI

I.A.A. concentration in g/ml	Curvature in degrees		
	series a	series b	series c
$0.5\ 10^{-7}$	11 ± 2	8 ± 1	9 ± 2
$0.6\ 10^{-7}$	15 ± 1	11 ± 2	12 ± 1
$0.7\ 10^{-7}$	13 ± 1	11 ± 1	12 ± 2
$0.8\ 10^{-7}$	15 ± 0	15 ± 1	16 ± 2
$0.9\ 10^{-7}$	16 ± 2	16 ± 1	15 ± 2
$1.0\ 10^{-7}$	16 ± 3	17 ± 2	16 ± 1
$1.1\ 10^{-7}$	18 ± 3	16 ± 2	18 ± 2
$1.2\ 10^{-7}$	19 ± 2	17 ± 2	17 ± 1
$1.3\ 10^{-7}$	19 ± 2	20 ± 1	20 ± 1
$1.4\ 10^{-7}$	19 ± 1	18 ± 2	17 ± 2
$1.5\ 10^{-7}$	21 ± 2	20 ± 1	19 ± 2

In this case too it is possible that the non-irradiated plants also have a first maximum of curvature, but then this should be situated at a lower I.A.A. concentration than was applied in these experiments. In this case the difference in behaviour observed between irradiated and non-irradiated plants might be accounted for by the hypothesis that the endogenous I.A.A. content of irradiated plants is lower than that of non-irradiated ones.

A second possibility is that irradiation with light of $\lambda = 660$ mμ stimulates the synthesis of a substance which causes the first maximum.

These two possibilities correspond with the possibilities 2 and 1 considered in the discussion on the straight-growth test (par. 2, see p. 12--13).

In order to investigate whether irradiation with light of $\lambda = 660$ mμ lowers the endogenous I.A.A. content or results in the enhanced synthesis of a new compound, extraction and quantitative analysis would be necessary. The results of such an analysis will be given in the next chapter.

4. Summary

It has been shown that irradiation with light of $\lambda = 660$ mμ causes an additional peak in the activity-concentration curve which is obtained if the growth of coleoptile sections or the curvature of coleoptiles is plotted against the I.A.A. concentration. This additional peak is situated at a low I.A.A. concentration.

CHAPTER V

QUANTITATIVE ANALYSIS OF THE I.A.A. CONTENT OF IRRADIATED AND NON-IRRADIATED COLEOPTILES

The purpose of this part of the investigation was to estimate the I.A.A. content of the coleoptiles. Destruction as well as formation of I.A.A. during extraction should be prevented; moreover, complications caused by the formation of auxin complexes should be avoided. The extraction method used in these experiments is based on that described by Terpstra (1953).

METHOD

Coleoptile tips of about 6 mm length were ground with some quartz sand; this was performed in orange light. The ground tissue was mixed with 5 ml of tap water at 100° C, frozen at about —5° C, and kept overnight at this temperature. The next day the mass was thawed and filtered. The tissue was rinsed with another 5 ml of tapwater. The 10 ml of extract thus obtained was made alkaline by adding about 10 mg $NaHCO_3$. Next it was shaken three times with 10 ml of ether, freed of peroxides. This ether fraction was discarded.

The aqueous residue was acidified with 0.1 N HCl, methyl orange being used as indicator (final pH ca 4), and shaken three times with 10 ml of ether. These ether fractions were evaporated, and the residue was dissolved once more in a small amount of ether.

This solution was applied to the starting line of a chromatogram. Sheets of Whatman No. 1 were used, and a mixture of isopropyl alcohol, 28 % ammonia and water (8: 1: 1) was employed as solvent. The chromatograms were developed with the solvent ascending for about 18 hours. A marker spot of I.A.A. was run parallel with the chromatogram of the extract.

After developing and drying, the strip of paper with the marker spot was removed and sprayed with a 1 % solution of cinnamic aldehyde in methanol. The strip was dried again and, when brought into a container with HCl-gas, showed the marker I.A.A. as a yellow-red spot. The Rf-value of I.A.A. ranged between 0.4 and 0.6.

The zone corresponding with the position of the I.A.A.-marker spot was cut from the chromatogram, and extracted with 3 × 10 ml of ether for 5 minutes at 37° C. The ether fractions were combined and evaporated, and the residue was transferred into an agar slice of 20 mm^3 in the manner described by TERPSTRA (1953). Next day the agar slices were cut into 6 blocks and tested on six coleoptiles.

EXPERIMENTS

The I.A.A.-content of tips of non-irradiated coleoptiles was compared by means of the curvature test with that of tips of plants, which $1\frac{1}{2}$ hours before the tips were collected had been irradiated with 700 ergs/cm^2 $\lambda = 660$ mμ. In Table XII the results of six experiments are given.

TABLE XII

Number of extracted tips	Curvature in degrees	
	extract from non-irradiated tips	extract from tips irradiated with light of $\lambda = 660$ mμ
50	15 ± 2	6 ± 1
10	13 ± 3	8 ± 1
30	29 ± 3	15 ± 2
10	34 ± 3	10 ± 1
10	34 ± 3	12 ± 2
40	36 ± 2	17 ± 2

In the course of $1\frac{1}{2}$ hours irradiation with light of $\lambda = 660$ mμ doubtlessly lowers the I.A.A. content of the coleoptile tips to about one half the original content. For the determination of I.A.A. from irradiated tips it appears necessary to extract about 10 tips to each 6 test plants. This matches the results of TERPSTRA (1953). It has not been investigated whether the differences in the size of the curvatures found in the various experiments of Table XII, are due to differences in the I.A.A. content of the extracted tips or to differences in the sensitivity of the testplants.

These results confirm the statement of VAN OVERBEEK (1936), that more auxin can be obtained from tips of non-irradiated coleoptiles than from tips of coleoptiles irradiated with orange light.

SUMMARY

Irradiation of Avena seedlings with light of 700 ergs/cm² $\lambda = 660$ mμ lowers the I.A.A. content of the tips of the coleoptiles in the course of $1\frac{1}{2}$ hours to about half the content found in the dark controls.

CHAPTER VI

EXTRACTION OF THE "RED LIGHT FACTOR" (R.L.F.)

Further investigations seemed desirable to make sure whether for the coleoptile the consequence of the irradiation with red light only consists in a decrease of the I.A.A.-content. If this would be so, the absence of the first peak in the growth-concentration curve of non-irradiated coleoptiles should be due to the fact that the hetero-auxin content of these coleoptiles is too high to allow the development of the first maximum, and then it would be impossible to introduce this first peak into the curve of the non-irradiated coleoptiles by adding an extract from irradiated ones, unless I.A.A. would be displaced by the extract from a surface to which it had been adsorbed. In the latter case it would depend on the ratio I.A.A. to extract which of these two would dominate, and then we should expect that the larger the amount of extract supplied to the coleoptiles, the larger the amount of I.A.A. would be that is required to obtain a similar effect. Thus the first growth peak should shift to higher I.A.A. concentrations when larger amounts of the extracted compound, henceforth called "Red Light Factor" or "R.L.F.", are supplied.

METHOD

Extracts from tips of irradiated seedlings were prepared and purified as described in chapter V. However, before the chromatogram was bio-assayed, the zone which, as indicated by an I.A.A.-marker spot, contains the I.A.A., was discarded. The eluates from the rest of the chromatogram were transferred into agar blocks that had been soaked in solutions of I.A.A. of various concentrations as it was supposed, in accordance with the results of the preceding experiments, that the effect of the 'R.L.F.' is observable only when it is applied in combination with I.A.A. The test plants were cultivated as described in chapter II. They were kept in darkness till the very moment of decapitation, and treated as described in chapter V.

EXPERIMENTS

First a chromatogram obtained with an extract from 300 tips cut from plants that had been irradiated for $1\frac{1}{2}$ hours with 700 ergs/cm² $\lambda = 660$ mμ, was tested on its activity. The chromatogram was divided into two halves by a cut parallel with the starting line, and each half was eluted and bio-assayed. Eluate *a* contained all the substances with Rf-values higher than that of I.A.A., eluate *b* the ones with Rf-values lower than that of I.A.A. Both eluates were tested in combination with I.A.A.-solutions of $\frac{1}{2} \times 10^{-7}$ and $\frac{3}{4} \times 10^{-7}$ g/ml.

TABLE XIII

I.A.A. concentration in g/ml	Control	Curvature in degrees	
		I.A.A. combined with eluate *a*	I.A.A. combined with eluate *b*
0.50×10^{-7}	11 ± 1	10 ± 1	11 ± 1
0.75×10^{-7}	11 ± 1	4 ± 1	11 ± 1

Table XIII, in which the curvatures of the test plants are given, shows that eluate *a* inhibited the curvature. Possibly it contained an active substance in more than optimum concentration.

The experiment was repeated with an extract made from 15 tips. Only the part of the chromatogram above the I.A.A. place was eluted, but it was first divided into 6 zones of 1.4 cm by cuts parallel to the starting line. The Rf-value of I.A.A. in this experiment was 0.56, the flow distance of the solvent 22.5 cm. The result is presented in Table XIV.

TABLE XIV

I.A.A. concentration in g/ml	Curvature in degrees
1×10^{-7}	15 ± 2
1×10^{-7} + zone 1 (front)	10 ± 1
1×10^{-7} + zone 2	10 ± 2
1×10^{-7} + zone 3	10 ± 1
1×10^{-7} + zone 4	7 ± 1
1×10^{-7} + zone 5	22 ± 4
1×10^{-7} + zone 6	8 ± 1

The eluate from zone 5, with slightly higher Rf-value than I.A.A. enhances the curvature induced by I.A.A. (10^{-7} g/ml) from about 15° to 22°.

Now it was tried to imitate the curvature-concentration curve found for irradiated plants by supplying non-irradiated plants with an eluate from a chromatogram in combination with I.A.A.

To this purpose extracts from coleoptile tips cut from plants that had been irradiated $1\frac{1}{2}$ hours previously with 700 ergs/cm² $\lambda = 660$ mμ, were freed from I.A.A. by chromatography. The zone containing I.A.A. was determined by means of a marker spot. The chromatogram above this zone was extracted and bio-assayed as a whole. Various amounts of the eluate were combined with various amounts of I.A.A., and the mixtures tested.

The results of three typical experiments are given in Table XV. Experiments II and III are plotted in Fig. 5.

TABLE XV

EXP. I

I.A.A. concentration in g/ml	Amount of extract added per test plant expressed in coleoptile tips		
	none	extract from 4/6 tip	extract from 8/6 tip
0.50 × 10⁻⁷	1 ± 1	4 ± 1	6 ± 1
1.00 × 10⁻⁷	9 ± 1	13 ± 1	16 ± 3
1.20 × 10⁻⁷	8 ± 2	10 ± 1	9 ± 1
1.40 × 10⁻⁷	13 ± 2	14 ± 2	9 ± 2
1.60 × 10⁻⁷	13 ± 2	15 ± 2	17 ± 3
1.80 × 10⁻⁷	17 ± 1	16 ± 2	17 ± 2
2.00 × 10⁻⁷	19 ± 1		
4.00 × 10⁻⁷	25 ± 0		

EXP. II

I.A.A. concentration in g/ml	Amount of extract added per test plant expressed in coleoptile tips			
	none	extr. fr. 2/6 tip	extr. fr. 4/6 tip	extr. fr. 8/6 tip
0.50 × 10⁻⁷	7 ± 2	7 ± 4	9 ± 2	9 ± 2
0.62 × 10⁻⁷	10 ± 1	14 ± 1	9 ± 1	10 ± 1
0.75 × 10⁻⁷	10 ± 1	19 ± 4	16 ± 2	11 ± 1
0.87 × 10⁻⁷	13 ± 2	12 ± 2	10 ± 3	5 ± 1
1.00 × 10⁻⁷	13 ± 2	15 ± 3	11 ± 2	12 ± 2
1.25 × 10⁻⁷	17 ± 2	20 ± 4	15 ± 2	13 ± 3

EXP. III

I.A.A. concentration in g/ml	Amount of extract added per test plant expressed in coleoptile tips			
	none	extr. fr. 2/6 tip	extr. fr. 4/6 tip	extr. fr. 8/6 tip
1.00 × 10⁻⁷	5 ± 1	6 ± 1	5 ± 2	6 ± 1
1.25 × 10⁻⁷	6 ± 1	7 ± 1	4 ± 1	5 ± 1
1.50 × 10⁻⁷	9 ± 2	9 ± 2	8 ± 3	8 ± 1
1.75 × 10⁻⁷	15 ± 2	15 ± 1	14 ± 4	15 ± 2
2.00 × 10⁻⁷	19 ± 3	11 ± 2	10 ± 2	9 ± 2
2.25 × 10⁻⁷	17 ± 3	17 ± 3	12 ± 1	12 ± 1
2.50 × 10⁻⁷	18 ± 3	14 ± 1	16 ± 2	15 ± 3

It appears that a purified extract from tips of irradiated coleoptiles transforms the one-peaked curvature-concentration curve of non-irradiated coleoptiles into a two-peaked one. Application of an amount of eluate equivalent with the extract from 1 tip is sufficient to obtain a maximum effect.

These experiments show that the R.L.F. can affect the response of non-irradiated test plants to growth substance. The I.A.A.-content

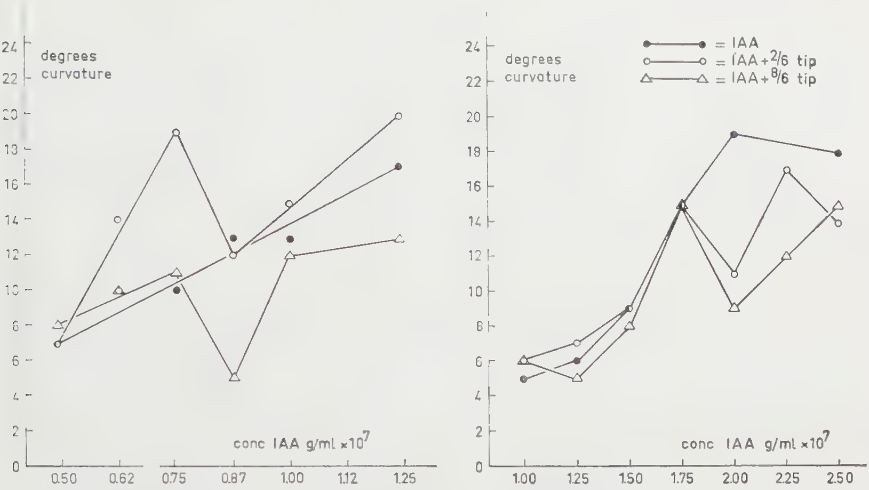

Fig. 5. Influence which a purified extract from coleoptiles irradiated with red light exercises on the curvature of non-irradiated coleoptiles.

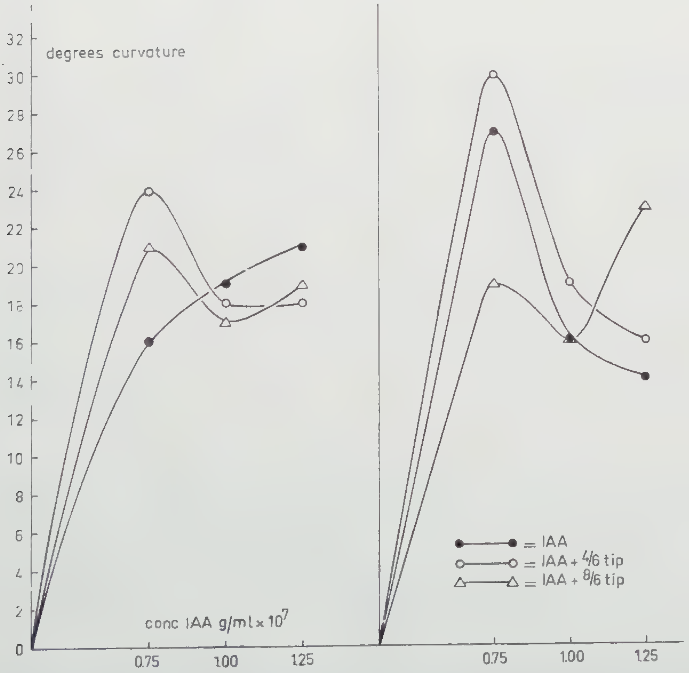

Fig. 6. Influence which a purified extract from coleoptiles irradiated with red light exercises on the curvature of test plants. Left: Test plants not irradiated. Right: Test plants irradiated with light of $\lambda = 660$ mμ.

of these plants therefore is not so high as to make them insensitive to the R.L.F. No evidence is found for the supposition that the first peak shifts to higher I.A.A. concentrations if larger amounts of R.L.F. are supplied. Either this is not so, or the shift is too small to be perceptible.

Finally the R.L.F. was tested in the same experiment on irradiated and non-irradiated plants. Table XVI, the figures of which are plotted in the graphs 6 and 7, shows the results.

TABLE XVI

EXP. I

Amount of extract added per test plant	I.A.A. concentration in g/ml	Not pre-illuminated	Pre-illuminated
none	0.75×10^{-7}	16 ± 3	27 ± 3
none	1.00×10^{-7}	19 ± 1	16 ± 1
none	1.25×10^{-7}	21 ± 2	14 ± 1
4/6 tip	0.75×10^{-7}	24 ± 2	30 ± 3
4/6 tip	1.00×10^{-7}	18 ± 2	19 ± 2
4/6 tip	1.25×10^{-7}	18 ± 3	16 ± 3
8/6 tip	0.75×10^{-7}	21 ± 3	19 ± 2
8/6 tip	1.00×10^{-7}	17 ± 2	16 ± 3
8/6 tip	1.25×10^{-7}	19 ± 2	23 ± 2

EXP. II

Amount of extract added per test plant	I.A.A. concentration in g/ml	Not pre-illuminated	Pre-illuminated
none	0.50×10^{-7}	8 ± 2	8 ± 2
none	0.75×10^{-7}	11 ± 2	17 ± 3
none	1.00×10^{-7}	26 ± 2	26 ± 3
2/6 tip	0.50×10^{-7}	7 ± 2	10 ± 1
2/6 tip	0.75×10^{-7}	15 ± 2	17 ± 3
2/6 tip	1.00×10^{-7}	19 ± 2	19 ± 3
4/6 tip	0.50×10^{-7}	12 ± 1	13 ± 2
4/6 tip	0.75×10^{-7}	17 ± 1	21 ± 2
4/6 tip	1.00×10^{-7}	17 ± 4	17 ± 2
8/6 tip	0.50×10^{-7}	0 ± 0	3 ± 1
8/6 tip	0.75×10^{-7}	18 ± 2	25 ± 2
8/6 tip	1.00×10^{-7}	16 ± 3	20 ± 2

In Fig. 6 (corresponding with experiment I) the graphs of the non-irradiated plants, either supplied with R.L.F. or not (a), are reproduced together with the graphs of the irradiated plants (b). In Fig. 7 (based on experiment II) however, the graphs of irradiated and non-irradiated testplants are plotted together, in Fig. 7a with no R.L.F. added, in Fig. 7b after addition of the R.L.F.-extract from 2/6 tip, in Fig. 7c from 4/6 tip and in Fig. 7d from 8/6 tip.

These experiments indicate that the R.L.F. enhances the curvature of non-irradiated and irradiated plants at the same exogenous I.A.A.-concentration, independent of the amount of R.L.F.

DISCUSSION

It appears impossible to attribute the absence of the first maximum in the curve presenting the size of the curvatures of non-irradiated test plants to their too high endogenous I.A.A.-level.

This appears from the fact that, by applying a purified extract from irradiated coleoptile tips, the development of such a first maximum can be obtained. Two possibilities for explaining the different behaviour of irradiated and non-irradiated coleoptiles are left:

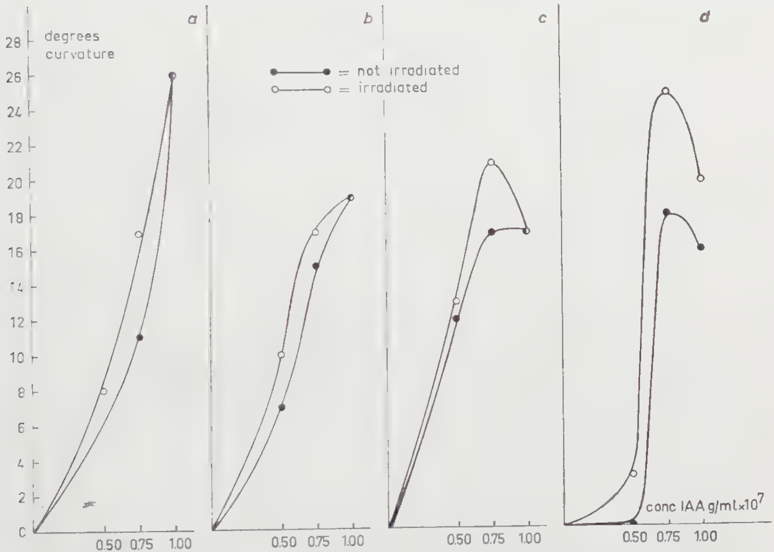

Fig. 7. Influence which a purified extract from coleoptiles irradiated with red light exercises on the curvature of test plants. *a*: No extract added. *b*: Each test plant supplied with extract from 2/6 tip. *c*: Each test plant supplied with extract from 4/6 tip. *d*: Each test plant supplied with extract from 8/6 tip.

Firstly, irradiation with light of $\lambda = 660$ mμ may cause or increase the formation of R.L.F.

Secondly, irradiation with light of $\lambda = 660$ mμ may enhance the capacity of the coleoptile to react to R.L.F. already present.

As an argument in support of the first explanation we may adduce the observation that "dark" coleoptiles can react to a supply of R.L.F., which would be difficult to conceive if the second explanation were the right one.

If irradiated coleoptiles contain more R.L.F. than non-irradiated ones, the supply of this substance required by irradiated coleoptiles in order to reach the "optimum" concentration, would be less than that required by the non-irradiated ones. This expectation was not fulfilled in our experiments, but this negative result may possibly be due to the limited range of concentrations that were tested.

SUMMARY

After irradiating seedlings with light of $\lambda = 660$ mμ it appeared possible to isolate from the coleoptile tips a compound (R.L.F.) which causes in the curve presenting the degree of curvature in non-irradiated coleoptiles the appearance of a similar first maximum (at low I.A.A. concentrations) as occurs naturally in that of the irradiated ones. The first peak in the curvature-concentration curve appears in this case in irradiated and non-irradiated coleoptiles at the same exogenous I.A.A. concentration, independent of the amount of R.L.F. supplied or already present (in the irradiated test plants).

CHAPTER VII

IDENTITY OF THE RED LIGHT FACTOR

1. DISCUSSION ON THE IDENTITY OF THE R.L.F.

With regard to the identity of the R.L.F. only vague indications can be given in this chapter.

1. It is probably an acid. This can be concluded from the fact that it can be transferred by shaking from an acidified aqueous solution into ether.

2. In experiments in which the R.L.F. was heated during two hours either in 1.5 N HCl or in 1.5 N KOH, it appeared that the R.L.F. is acid proof, but that it looses its activity if it is boiled with alkali. The experiment was made according to the method of TERPSTRA (1953). The curvatures induced by mixtures of I.A.A. and the R.L.F. either untreated or treated with acid or alkali, are given in Table XVII.

TABLE XVII

I.A.A. concentration in g/ml	Control	Curvature in degrees after the addition of extract from one tip per test plant		
		untreated	boiled with acid	boiled with alkali
0.75×10^{-7}	21 ± 2	8 ± 1	8 ± 2	27 ± 3
1.00×10^{-7}	28 ± 3	14 ± 1	16 ± 2	28 ± 2
1.25×10^{-7}	29 ± 2	19 ± 1	20 ± 3	30 ± 3

The amounts of R.L.F. that were applied in this series of experiments, were considerably higher than those used in the experiments of chapter VI.

3. If the R.L.F. is applied to Avena coleoptiles, without addition of I.A.A. it causes no curvatures. For this reason it is improbable that the R.L.F. is identical with KÖGL's auxin-a. This would be possible only in the event that KÖGL's auxin preparation had been polluted with so large an amount of I.A.A. that the curvatures induced by solutions of this preparation might be ascribed to an additive activity of I.A.A. and auxin-a, but as his preparation was a highly purified one, this is hardly conceivable.

4. BRIAN and HEMMING (1957 and 1958) found that pea epicotyls fail to respond to gibberellic acid if there is no I.A.A. in the culture solution. Gibberellic acid enhanced the growth-promoting activity of

I.A.A. at all the I.A.A. concentrations that were tested. This is not in conformity with the way in which the R.L.F. interacts with I.A.A. Moreover gibberellic acid is not acid proof.

Yet it seemed worth while to determine the Rf-value of gibberellic acid in our chromatograms, and to investigate the activity of gibberellic acid in the straight-growth test and in the curvature test.

2. Determination of the Rf-value of gibberellic acid

4 μg gibberellic acid was mixed with 4 μg I.A.A. and chromatographed as described in chapter V. After being developed, the chromatogram was dried, sprayed with 1 % H_2SO_4 in methanol, and dried again at 60° C during 10 minutes. After this treatment the spot of gibberellic acid can be seen in U.V. light.

The I.A.A. spot was detected on a parallel strip of the chromatogram as described in chapter V.

The results of 5 experiments can be seen in Table XVIII.

TABLE XVIII

The Rf-values for:

I.A.A.	Gibberellic acid	R.L.F.
0.35	0.52	
0.49	0.59	
0.34	0.54	> 0.45
0.31	0.48	
0.62	0.74	

It appears that the Rf-value of gibberellic acid ranges from 0.5 to 0.7. So this compound is to be found, like the R.L.F., somewhat nearer to the front than I.A.A.

Thus the Rf-value of gibberellic acid does not exclude in advance the possibility that the R.L.F. is identical with gibberellic acid.

3. Activity of gibberellic acid; curvature test

For these experiments agar slices were soaked in mixtures of I.A.A. and gibberellic acid. Preliminary tests showed that 10^{-6} g/ml and 1.5×10^{-6} g/ml gibberellic acid were concentrations suitable for our purpose. The agar blocks were tested on once decapitated Avena coleoptiles. The coleoptiles were cultivated and tested as described in chapter V, and were kept in absolute darkness till the moment of decapitation.

Table XIX shows the curvatures of the test plants two hours after application of the agar blocks; two experiments were made. Experiment II is plotted in Fig. 8 (left).

Obviously gibberellic acid can induce at low I.A.A. concentrations an additional peak in the curvature-concentration curve.

4. Straight-growth test with I.A.A. combined with gibberellic acid

Finally some cylinder tests were carried out with mixed solutions of I.A.A. and of gibberellic acid. The method is described in chapter III.

TABLE XIX

I.A.A. concentration in g/ml	Curvature in degrees concentration of gibberellic acid in g/ml		
	0.	10^{-6}	1.5×10^{-6}
EXP. I			
0.6×10^{-7}	12 ± 2	11 ± 2	11 ± 2
0.7×10^{-7}	11 ± 1	11 ± 3	13 ± 3
0.8×10^{-7}	14 ± 2	20 ± 2	17 ± 1
0.9×10^{-7}	23 ± 1	15 ± 2	15 ± 0
1.0×10^{-7}	26 ± 1	17 ± 2	21 ± 3
1.1×10^{-7}	23 ± 2	23 ± 2	22 ± 3
1.2×10^{-7}	23 ± 1	23 ± 2	26 ± 2
1.3×10^{-7}	24 ± 1	25 ± 2	26 ± 2
EXP. II			
0.62×10^{-7}	5 ± 1	9 ± 2	8 ± 2
0.75×10^{-7}	7 ± 0	4 ± 1	4 ± 2
0.87×10^{-7}	9 ± 2	10 ± 2	7 ± 2
1.00×10^{-7}	12 ± 1	19 ± 2	7 ± 1
1.12×10^{-7}	13 ± 2	13 ± 2	7 ± 2
1.25×10^{-7}	10 ± 2	7 ± 1	6 ± 2
1.37×10^{-7}	12 ± 2	19 ± 2	16 ± 1

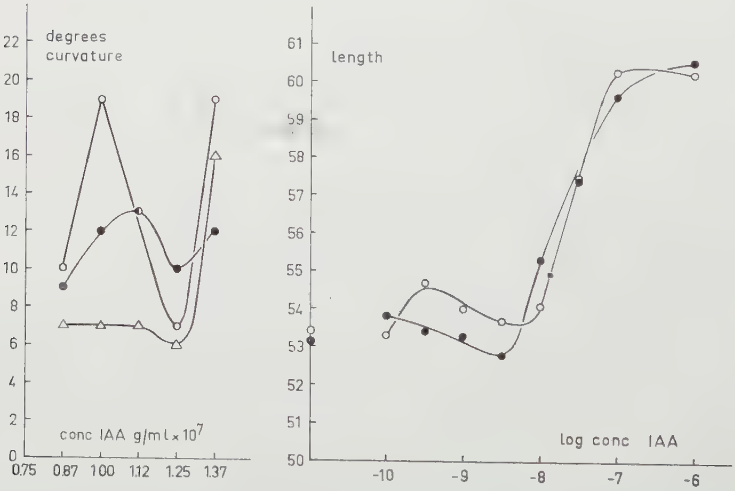

Fig. 8. Influence of gibberellic acid. Left: in the curvature test, right: in the cylinder test; dots: no G.A. added; circle: 10^{-6} g/ml G.A.; triangle: 1.5×10^{-6} g/ml G.A.

The coleoptiles that were to be cut into sections in orange light, were not pre-illuminated with red or orange light.

In Table XX the length reached by the sections during the three hours they floated on the surface of the solutions, is presented in scale units; two experiments were made. Experiment II is plotted in Fig. 8 (right).

TABLE XX

I.A.A. concentration in g/ml	Final length of sections in scale units			
	EXP. I Concentration of gibberellic acid in g/ml		EXP. II Concentration of gibberellic acid in g/ml	
	0.	10^{-6}	0.	10^{-6}
0.	52.5 ± 0.2	52.7 ± 0.1	53.1 ± 0.3	53.4 ± 0.2
1.10^{-10}	53.0 ± 0.2	52.9 ± 0.3	53.8 ± 0.3	53.3 ± 0.2
3.10^{-10}	52.3 ± 0.3	53.0 ± 0.3	53.4 ± 0.2	54.7 ± 0.2
1.10^{-9}	51.3 ± 0.2	52.8 ± 0.2	53.3 ± 0.1	54.0 ± 0.2
3.10^{-9}	53.7 ± 0.3	53.1 ± 0.3	52.8 ± 0.2	53.7 ± 0.3
1.10^{-8}	54.1 ± 0.3	53.5 ± 0.3	55.3 ± 0.3	54.1 ± 0.2
3.10^{-8}	56.3 ± 0.6	55.5 ± 0.4	57.4 ± 0.5	57.5 ± 0.5
1.10^{-7}			59.6 ± 0.7	60.3 ± 0.7
1.10^{-6}			60.5 ± 0.7	60.2 ± 0.8

Gibberellic acid indeed enhances the growth of the sections at low I.A.A. concentrations, and consequently produces an additional peak in the graph.

SUMMARY

The activity of gibberellic acid in the curvature test and in the straight-growth test as well as its place in the chromatogram are comparable to those of the R.L.F. This, however, is not sufficient to prove the identity of the two compounds.

CHAPTER VIII

THE R.L.F. IN CONNECTION WITH THE PHOTOTROPIC REACTIONS OF AVENA COLEOPTILES

As shown by ARISZ (1915) the phototropic curvature of Avena coleoptiles is a periodic function of the light energy provided that the latter is supplied within a short time. With increasing amounts of light under these circumstances a first positive, a negative and a second positive curvature are produced. These different responses may be attributed to

a. a redistribution of auxin due to a lateral shift of the auxin transport to the shade side,
b. an inactivation of auxin by the light,
c. an increase in the auxin synthesis at higher light intensities,
d. a reduced response of cells to auxin under the influence of the light.

Arguments for and against each of these possibilities were reviewed by SCHRANK (1950) and WENT (1956). By none of the investigators whose experiments had a bearing on the question of the cause of these differences in phototropic behaviour, the influence of red light was taken into account.

Now it was shown in the preceding chapters that the growth of a coleoptile which is irradiated with light of $\lambda = 660$ mμ decreases with decreasing I.A.A. concentrations, but increases again at low I.A.A. concentrations before it is reduced to zero. This relation between growth and I.A.A. concentration curve is represented tentatively by one of the curves shown in Fig. 9. (broken line).

The curve for the plants that were not pre-illuminated (solid line), has been based on the data obtained by the experiments discussed in this chapter, as will be shown on p. 31.

Fig. 9 seems to offer a new possibility for the explanation of the negative and the second positive curvature.

Let it be assumed, with Oppenoorth (1941), that the auxin content of the coleoptile decreases with increasing quantities of blue light. As the irradiated side of the coleoptile receives larger amounts of blue light than the shade side, the illuminated side will contain less auxin than the shade side. Now with increasing amounts of unilateral light energy the I.A.A. content of the light side as well as that of the shade side can be imagined to move along the graph of Fig. 9 to the left, that of the light side preceding that of the shade side.

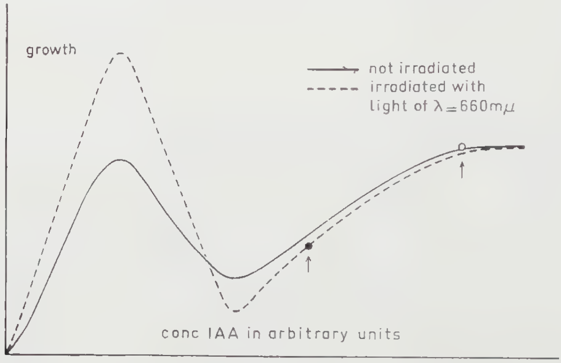

Fig. 9. Tentative course of the growth rate curve of intact coleoptiles at different I.A.A. concentrations. circle: I.A.A. level of non-irradiated plants; dot: I.A.A. level of plants irradiated with red light.

At the outset (at low light energy, i.e. at a high but decreasing auxin content of the coleoptile) the growth of the light side may be less than the growth of the shade side (first positive curvature). When mounting the slope towards the first peak from the right side of the graph, however, the growth rate of the light side may surpass the growth rate of the shade side (negative curvature) whereas, when the first peak has been passed, the tables are once more turned (second positive curvature).

This supposition could be checked by investigating the influence which a pre-illumination with light of $\lambda = 660$ mμ exercises on the growth rate of a coleoptile whose phototropic reaction lies at the turning point from the negative to the second positive curvature. If this turning point really corresponds with the first peak of the curve which presents the relation between growth and I.A.A. concentration, the growth rate of coleoptiles should at this point be enhanced by an irradiation with light of $\lambda = 660$ mμ.

In the same series of experiments the influence which irradiation with light of $\lambda = 660$ mμ and of $\lambda = 480$ mμ and with combinations of these wave lengths exercises on the straight growth of coleoptiles, was studied also in the regions of the first positive and negative curvature.

METHOD

The coleoptiles were cultivated as described in chapter II for the experiments on phototropism. When the seedlings were 88 hours old, a particle of vermiculite was fixed by means of lanoline on the coleoptile at a distance of about 1 cm from the tip; this operation was performed in green light of $\lambda = 560$ mμ; the particle was to serve as mark. Next the coleoptiles were photographed by use of light of $\lambda = 560$ mμ, and irradiated unilaterally with light of $\lambda = 660$ mμ, $\lambda = 480$ mμ or both.

Two hours after the irradiation the coleoptiles were photographed again. The increase in length of the coleoptiles from tip to mark was measured in mm.

EXPERIMENTS

The results of these experiments are recorded in Table XXI. The result of one of them is plotted in Fig. 10.

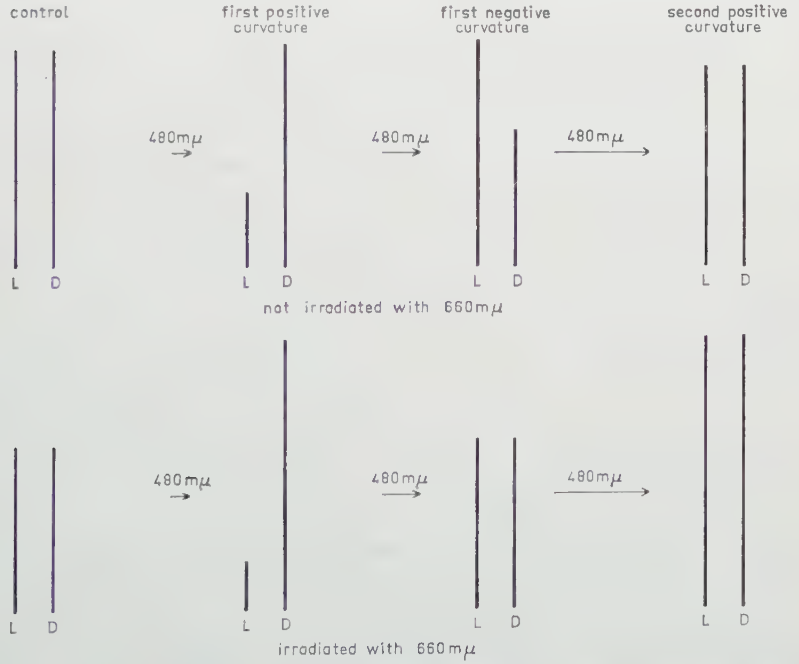

Fig. 10. Increase in length in 2 hours of the light side (L) and of the shade side (D) of coleoptiles that were one-sidedly illuminated with blue light of various intensities; the coleoptiles of the lower row previously irradiated with light of 660 mμ, those of the upper row not previously irradiated.

TABLE XXI

Growth in mm during 2 hours after different irradiations

Region of the *first positive* phototropic curvature

	No light of $\lambda = 480$ mμ	20 ergs/cm^2 $\lambda = 480$ mμ	
		light side	shade side
not pre-illuminated	0.55 ± 0.06 (8)	0.12 ± 0.04 (16)	0.49 ± 0.06 (16)
pre-illuminated with 700 ergs/cm^2 $\lambda = 660$ mμ	0.40 ± 0.04 (23)	0.21 ± 0.04 (17)	0.66 ± 0.06 (17)
not pre-illuminated	0.57 ± 0.05 (20)	0.20 ± 0.04 (7)	0.59 ± 0.08 (7)
pre-illuminated with 700 ergs/cm^2 $\lambda = 660$ mμ	0.43 ± 0.07 (12)	0.13 ± 0.05 (9)	0.71 ± 0.09 (9)

Region of the *negative* phototropic curvature

	No light of $\lambda = 480$ mμ	4800 ergs/cm^2 $\lambda = 480$ mμ	
		light side	shade side
not pre-illuminated	0.57 ± 0.05 (20)	0.60 ± 0.16 (8)	0.36 ± 0.08 (8)
pre-illuminated with 700 ergs/cm^2 $\lambda = 660$ mμ	0.43 ± 0.07 (12)	0.45 ± 0.08 (8)	0.45 ± 0.08 (8)
not pre-illuminated	0.55 ± 0.06 (18)	0.50 ± 0.17 (3)	0.30 ± 0.17 (3)

Transition region from *negative* to *second* positive phototropic curvature

	No light of $\lambda = 480$ mμ	24000 ergs/cm^2 $\lambda = 480$ mμ	
		light side	shade side
not pre-illuminated	0.50 ± 0.06 (12)	0.56 ± 0.05 (14)	0.56 ± 0.05 (14)
pre-illuminated with 700 ergs/cm^2 $\lambda = 660$ mμ		0.72 ± 0.06 (15)	0.72 ± 0.06 (15)
not pre-illuminated	0.58 ± 0.05 (15)	0.53 ± 0.12 (06)	0.53 ± 0.12 (06)
pre-illuminated with 700 ergs/cm^2 $\lambda = 660$ mμ		0.77 ± 0.04 (17)	0.77 ± 0.04 (17)
not pre-illuminated		0.78 ± 0.04 (11)	0.78 ± 0.04 (11)
pre-illuminated with 700 ergs/cm^2 $\lambda = 660$ mμ		0.97 ± 0.08 (12)	0.97 ± 0.08 (12)

It appears that:

a. irradiation with 700 ergs/cm^2 $\lambda = 660$ mμ alone inhibits the growth of the coleoptiles;

b. unilateral light of $\lambda = 480$ mμ (20 ergs/cm^2) if given to coleoptiles not irradiated with $\lambda = 660$ mμ, inhibits growth at the light side only, but in coleoptiles pre-irradiated with $\lambda = 660$ mμ, it enhances in addition the growth rate at the shade side;

c. in the region of the negative curvature the growth of the shade side is inhibited;

d. at the turning point from negative to second positive curvature a previous illumination with light of $\lambda = 660$ mμ enhances the growth rate of the coleoptiles; the growth rate of these pre-illuminated coleoptiles is also larger than that of controls kept in complete darkness.

DISCUSSION

Table XXI shows that with increasing quantities of unilateral blue light the growth at the light side first passes a minimum (first positive curvature) and that then the growth at the shade side too passes a minimum (negative curvature). This holds true for coleoptiles, no matter whether they are pretreated or not pretreated with red light. This fits in with the hypothesis that was expounded in the introduction to this chapter and according to which the growth of light and shade side can be schematically represented by the graph of Fig. 9. Moreover irradiation with light of $\lambda = 660$ mμ enhances the growth of the coleoptiles in the transition region between the negative and the second positive curvature. So the growth of light and shade side of coleoptiles not irradiated with light of $\lambda = 660$ mμ runs along the solid graph of Fig. 9, whereas the growth of coleoptiles pre-irradiated with light of $\lambda = 660$ mμ is indicated by the broken line. Indeed, there is a striking resemblance between the growth pattern shown by the coleoptiles under influence of increasing quantities of blue light and that shown by them under the influence of decreasing quantities of I.A.A. However, in the introduction to this chapter we assumed that by increasing the quantities of blue light the I.A.A. content of the coleoptile decreases. If this is right, the negative and second positive curvature must be due to the activity of the R.L.F. Unfortunately, the results of the experiments by the aid of which OPPENOORTH (1941) thought that he could prove the inactivation of auxin by blue light, have lost their convincing character since TERPSTRA (1953) demonstrated that Oppenoorth's method of auxin extraction is not reliable. Secondly, OPPENOORTH estimated the overall auxin content of his extracts in the manner that was usual at that time, and not the I.A.A. content itself (i.e. after chromatographic separation). So the evidence, advanced thus far, should be completed by a determination of the I.A.A. content of coleoptiles irradiated with 24 000 ergs/cm^2 $\lambda = 480$ mμ, that is at the transition of the negative to the second positive curvature.

The experiments of Table XXI show that at the turning point of positive and negative curvature coleoptiles which are not irradiated with red light, nevertheless show a first growth peak, though a less pronounced one than is shown by coleoptiles that have been irradiated with red light. This is indicated by the solid line of Fig. 9. Presumably either decapitation and sectioning of the coleoptiles obliterate this less pronounced peak, or large quantities of blue light have the same effect as red light in producing a first growth peak.

From these experiments information is obtained also on the cause of the first positive curvature. They confirm the observation of BEYER (1927) that with the first positive curvature the growth at the irradiated side of the coleoptile is inhibited, the growth at the dark side on the other hand enhanced. It appears, however, that this enhancement of the shade side occurs only in pre-irradiated coleoptiles. The most plausible explanation is the classic one, viz. that the unilateral blue light causes an accumulation of the available auxin at the shade side of the coleoptile. That this accumulation would not occur with coleoptiles that have not been irradiated with red light, is unlikely. Maybe the difference in the reaction of irradiated and non-irradiated coleoptiles is connected with the reduction of the I.A.A. content of the coleoptiles by red light. Possibly the I.A.A. level of the non-irradiated coleoptiles is above the optimum so that an increase of the I.A.A. content at the shade side cannot result in an enhancement of the growth rate. So in our opinion the first positive curvature is due to a shift of I.A.A. towards the shade side; the negative and the second positive curvature to a reduction of the I.A.A. content at both light and shade side of the coleoptile, which brings the coleoptile into the action region of the R.L.F., possibly combined with an accumulation of I.A.A. This is in line with the views of WENT (1956).

This chapter may end with a short contemplation of the changes in "disposition" ("Stimmung" or "tonus"), i.e. the changes which the power to react to a stimulus undergoes under the influence of a preceding stimulus. ARISZ (1914) stated that the duration and the intensity of a preceding all-round illumination determine the way in which the coleoptile reacts on a following one-sided light stimulus. By pre-illumination with white light the plant can reach a stage in which it reacts on a unilateral illumination by a negative curvature. With a longer duration of the pre-illumination the faculty to produce a positive curvature returns. In our opinion pre-illumination reduces the I.A.A. content of the coleoptile. If it is true that the I.A.A. level determines whether a positive or a negative curvature will result, the so called phototonus of a coleoptile must entirely depend upon its I.A.A. level.

SUMMARY

In this chapter evidence is adduced for the hypothesis that the first positive curvature is due to a shift of heteroauxin to the dark side of the coleoptile; the negative and the second positive curvature on the other hand would be due to a reduction of the I.A.A. level in the coleoptile as a result of which the red light factor gets the opportunity to influence growth. Consequently the red light factor can influence not only the growth rate but the phototropic response as well.

CHAPTER IX

THE INFLUENCE OF FAR RED LIGHT (of $\lambda = 740$ mμ) ON THE AVENA COLEOPTILE

In several instances an antagonistic effect of red and far red light has been found.

In the preceding chapters it was shown that light of $\lambda = 660$ mμ (red light) has two different and probably independent effects on the Avena coleoptile,

firstly: the I.A.A. content of the coleoptile is decreased; the higher maximum reached by the first positive phototropic curvature is presumably connected with this decrease;
secondly: at low I.A.A. concentrations a second growth maximum is induced, which causes an increase in the rate of growth of the coleoptiles at the turning point between the negative and the second positive phototropic curvature.

It seemed worth while to investigate whether irradiation with light of $\lambda = 740$ mμ (far red light) antagonizes one of these effects or perhaps even both.

The methods used to this end were the same as those described in the preceding chapters far the corresponding experiments on the influence of red light.

EXPERIMENTS

First effect

a. Avena coleoptiles were unilaterally irradiated with 20 ergs/cm² $\lambda = 480$ mμ in order to produce a maximum positive curvature. They were pre-illuminated either with 700 ergs/cm² $\lambda = 660$ mμ or with 6000 ergs/cm² $\lambda = 740$ mμ or with both. In Table XXII the resulting curvatures are shown.

TABLE XXII

Phototropic curvature (in degrees) induced by a unilateral illumination with 20 ergs/cm² $\lambda = 480$ mμ without or after a pre-illumination with

	EXP. I	EXP. II	EXP. III
—	9.0 ± 0.8 (14)	12.6 ± 0.9 (10)	9.9 ± 0.9 (7)
700 ergs/cm² $\lambda = 660$ mμ	13.3 ± 1.4 (09)	17.1 ± 1.8 (08)	14.0 ± 1.8 (5)
700 ergs/cm² $\lambda = 660$ mμ + 6000 ergs/cm² $\lambda = 740$ mμ	12.2 ± 1.3 (10)	20.7 ± 0.8 (11)	13.4 ± 0.8 (5)
	EXP. IV	EXP. V	EXP. VI
—	12.3 ± 1.4 (7)	9.9 ± 0.9 (7)	8.6 ± 1.1 (8)
6000 ergs/cm² $\lambda = 740$ mμ	16.2 ± 1.3 (6)	15.4 ± 1.4 (5)	14.0 ± 0.8 (8)

It appears that illumination with light of $\lambda = 740$ mμ does not reverse the effect of illumination with light of $\lambda = 660$ mμ. On the contrary, it has the same effect, viz. a larger maximum curvature.

b. The same conclusion can be drawn from experiments on the influence which light of $\lambda = 740$ mμ exercises on the absolute growth of the coleoptiles in the region of the first positive curvature. Like light of $\lambda = 660$ mμ, it inhibits the growth of coleoptiles that were not subjected to unilateral blue light (Table XXIII), and it increases the growth at the shade side of coleoptiles that are developing a phototropic curvature after an unilateral irradiation with 20 ergs/cm² $\lambda = 480$ mμ.

TABLE XXIII

Growth of the light and shade side (in scale units) after unilateral irradiation

	No light of $\lambda = 480$ mμ	Light side	Shade side
no pre-illumination	0.58 ± 0.08 (20)	0.13 ± 0.04 (14)	0.62 ± 0.05 (14)
pre-illuminated with 6000 ergs/cm^2 $\lambda = 740$ mμ	0.46 ± 0.08 (12)	0.07 ± 0.03 (11)	0.66 ± 0.07 (11)
no pre-illumination	0.57 ± 0.05 (20)	0.20 ± 0.04 (7)	0.59 ± 0.08 (7)
pre-illuminated with 6000 ergs/cm^2 $\lambda = 740$ mμ	0.46 ± 0.09 (10)	0.22 ± 0.06 (12)	0.93 ± 0.09 (12)

c. Finally it could be proved that light of $\lambda = 740$ mμ reduces the I.A.A. content of Avena coleoptiles in the same way as light of $\lambda = 660$ mμ does; this is shown in Table XXIV.

TABLE XXIV

Curvature test of extracts

Extract from	Non-irradiated coleoptiles	Coleoptiles irradiated with 6000 ergs/cm^2 $\lambda = 740$ mμ
30 tips	10 ± 3	4 ± 0.5
20 tips	8 ± 2	3 ± 1
20 tips	7 ± 2	1 ± 1

Second effect

a. By application of the straight growth test (compare chapter IV) we studied the influence which light of $\lambda = 740$ mμ exercises on the first peak of the curve which presents growth as a function of the I.A.A. concentration in coleoptiles that have been irradiated with light of $\lambda = 660$ mμ. In Table XXV the final lengths of coleoptile sections at the critical I.A.A. concentrations are given in scale units. It appears that the growth-enhancing effect of light of $\lambda = 660$ mμ is completely or partly neutralized by illumination of the seedlings with light of $\lambda = 740$ mμ.

TABLE XXV

Growth of coleoptile cylinders in solutions of I.A.A.

	in a concentration of			
	10^{-9} g/ml		3.10^{-9} g/ml	
	I	II	I	II
not pre-illuminated	52.6 ± 0.2	51.2 ± 0.2	51.4 ± 0.3	51.3 ± 0.3
pre-illuminated with 700 ergs/cm^2 $\lambda = 660$ mμ	53.3 ± 0.2	52.7 ± 0.3	52.6 ± 0.1	53.5 ± 0.3
pre-illuminated with 6000 ergs/cm^2 $\lambda = 740$ mμ + 700 ergs/cm^2 $\lambda = 660$ mμ	52.8 ± 0.3	51.9 ± 0.2	52.0 ± 0.3	52.3 ± 0.1

b. Finally it was investigated whether irradiation with light of $\lambda = 740$ mμ reverses the effect which light of $\lambda = 660$ mμ exercises on the growth of coleoptiles in the transition region between the negative and the second positive phototropic curvature. To this end coleoptiles were pre-illuminated either with 700 ergs/cm^2 λ 660 mμ or with 700 ergs/cm^2 $\lambda = 660$ mμ immediately followed by 6000 ergs/cm^2 $\lambda = 740$ mμ and then irradiated one-sidedly with 24000 ergs/cm^2 $\lambda = 480$ mμ (see chapter VIII). Table XXVI gives the increase in length of the coleoptiles two hours after this treatment. It can not be doubted that the effect of light of $\lambda = 660$ mμ is annihilated by light of 740 mμ.

TABLE XXVI

Growth of coleoptiles after an irradiation with

Pre-illumination	No light of $\lambda = 480$ mμ	24000 ergs/cm^2 $\lambda = 480$ mμ
none	0.45 ± 0.06 (11)	0.40 ± 0.05 (15)
700 ergs/cm^2 $\lambda = 660$ mμ		0.64 ± 0.07 (15)
700 ergs/cm^2 $\lambda = 660$ mμ + 6000 ergs/cm^2 $\lambda = 740$ mμ		0.47 ± 0.07 (12)

DISCUSSION

Irradiation with light of $\lambda = 740$ mμ antagonizes the effect of light of $\lambda = 660$ mμ on the growth peak at low I.A.A. concentrations that appears in the curve which presents growth as a function of the I.A.A. concentration. The influence which light of $\lambda = 660$ mμ exercises on coleoptiles in the transition region between the negative and the second positive phototropic curvature too is antagonized by light of $\lambda = 740$ mμ. This finding is another argument in favour of our attempt to link up the phenomena of the negative and second positive curvature with the occurrence of a first growth peak, i.e. the one found at low I.A.A. concentrations. Illumination with light of $\lambda = 740$ mμ and with light of $\lambda = 660$ mμ, however, have the same effect on the growth of coleoptiles, that were not exposed to unilateral blue light, as they have on the first positive curvature and on the I.A.A. content. It therefore may be concluded that the hypothesis that a relation exists between some of the effects of red light, viz. the enhancement of the first positive curvature, the decrease of the growth rate, and the decrease of the I.A.A. content, gains in probability.

A twofold effect of far red light was found also by De Lint (1957). In his experiments on the effect which irradiation excercises on the final length of Avena coleoptiles, far red irradiation decreased the length as compared to that of non-irradiated coleoptiles, but it partly reversed the inhibition induced by red or yellow light.

Now our Fig. 3 shows that the introduction, by irradiation with red light, of a first peak in the curve which presents growth as a function of the I.A.A. concentration, is accompanied by the introduction of a depression at somewhat higher I.A.A. concentrations. Fig. 5 shows that a similar depression is caused by the R.L.F. extract and that the depression is the more pronounced the higher the amount of R.L.F. As irradiation with far red light annihilates the first growth peak caused by the R.L.F., it will, in all probability, also annihilate the growth depression due to the R.L.F. Presumably De Lint has reduced the I.A.A. content of his coleoptiles by irradiation with red or yellow light to the level where the R.L.F. causes the growth depression discussed above, and he has abolished the depression with far red light. Since far red light, as well as red light, reduces the I.A.A. content of the coleoptile, it must be impossible that the final length of the dark controls is attained by coleoptiles that have been exposed to a far red irradiation. De Lint found that they do not do this.

Summary

One of the two effects of red light on the Avena coleoptile is neutralized by far red light, namely the transformation of the one-peaked curve which presents growth as a function of the I.A.A. into a two-peaked one.

On the other hand far red light has the same depressing effect as red light on the growth rate of non-illuminated coleoptiles and on the maximum of the first positive phototropic curvature.

CHAPTER X

CONSEQUENCES WHICH THE DISCOVERY OF THE INFLUENCE EXERCISED BY RED AND ORANGE LIGHT ON AVENA COLEOPTILES HAS FOR THE APPLICATION OF AUXIN TESTS

In the preceding chapters it was shown that orange and red light influence the reactions of the coleoptile on I.A.A., and that this influence is exercised via the primary leaf. Without intending a further comprehensive analysis we performed some experiments in order to learn the effect of orange light on the results of the curvature test.

I

Usually one switches on the orange light when entering the dark-room with the intention to carry out a curvature test. In consequence the last seedlings to be decapitated have much more time to react on the orange light than the first ones because, as has been shown above, the seedling reacts only so long as the primary leaf remains intact. If it can be shown that this commercial practice influences the curvatures of the test plants, one should operate carefully when using orange light. We investigated this in the next experiments.

At the beginning of the experiment the racks with coleoptiles that were to be tested, were all illuminated at the same time with orange light. The curvature test was carried out as usual, i.e. the plants were decapitated twice with an interval of two hours. The primary leaf was removed after the first decapitation. The subsequent treatments were applied first to series *a*, next to series *b*. There was an interval of 30 minutes between the treatment of the first rack of series *a* and that of the first rack of series *b*.

TABLE XXVII

Effect of orange light on the standard Avena (curvature) test

I.A.A. concentration in g/ml	Curvature in degrees	
	series *a*	series *b*
0.	—1 ± 0	—2 ± 1
0.25 10^{-7}	9 ± 1	7 ± 1
0.50 10^{-7}	11 ± 2	12 ± 1
0.75 10^{-7}	16 ± 1	13 ± 1
1.00 10^{-7}	20 ± 1	16 ± 1
1.25 10^{-7}	15 ± 2	14 ± 1

Table XXVII gives the curvatures of the plants two hours after the application of the agar blocks with I.A.A. In series *b* the maximum curvature is decreased as compared to series *a*. If this test method is used to compare quantities of auxin, the use of orange light therefore is apt to pervert the results. This source of error can be eliminated by keeping the test plants in the dark till the very moment of decapitation.

II

With the standard curvature test it is usual to decapitate the coleoptiles twice; this practice is based on the finding of VAN DER WEY (1931) that the sensitivity to auxin is enhanced by a second decapitation. After the first decapitation the primary leaf is usually loosened, though VAN DER WEY did not indicate whether he did this or not.

Now we made it our point to find out whether the "increase in sensitivity" (by which VAN DER WEY denoted the fact that at low auxin concentrations larger curvatures were obtained) is due to the second decapitation or to the circumstance that the removal of the primary leaf was postponed.

Four series of plants were tested with the same series of dilutions of a I.A.A. solution. Each rack of plants was kept in darkness till its turn for decapitation had come.

Series a was decapitated twice with an interval of 1½ hours. The primary leaf was pulled out in the usual way after the first decapitation.

Series b was treatened like series *a*, but the primary leaf was not loosened until after the second decapitation.

Series c was decapitated once. The primary leaf was pulled out immediately after decapitation, but the agar blocks were applied after 1½ hours to make this series comparable to series *a*.

Series d like *c*, but the I.A.A. was applied immediately after decapitation.

The results are recorded in Table XXVIII.

The largest curvatures at low I.A.A. concentrations are not to be found in series *a*, but this series shows the best proportionality between curvature and I.A.A. concentration. Obviously a second decapitation does not enhance the reaction to low concentrations of I.A.A. Probably VAN DER WEY came to this conclusion by comparing a series *d* with

TABLE XXVIII

I.A.A. concentration in g/ml	Curvature in degrees			
	a	*b*	*c*	*d*
0.50×10^{-7}	7 ± 2	11 ± 2	9 ± 2	7 ± 1
0.75×10^{-7}	10 ± 2	13 ± 2	15 ± 2	10 ± 2
1.00×10^{-7}	12 ± 2	15 ± 1	15 ± 2	14 ± 2
1.25×10^{-7}	16 ± 2	15 ± 1	17 ± 2	12 ± 2
1.50×10^{-7}	17 ± 2	13 ± 1	18 ± 1	14 ± 1
2.00×10^{-7}	19 ± 2	20 ± 2	18 ± 1	18 ± 1
2.50×10^{-7}	17 ± 2	18 ± 2	17 ± 1	23 ± 5

a series *b*. Indeed series *b* responds more vigorously than series *d* to small amounts of I.A.A., but this is caused by the fact that in series *b* the primary leaf was left intact during 1½ hours after the beginning of illumination, and not by the second decapitation. This appears from a comparison between series *a* and series *c*, which shows that the second decapitation decreases the "sensivity" instead of enhancing it.

So if a good proportionality between curvature and I.A.A. concentration is wanted, one should decapitate twice, but if very sensitive plants are needed, one should decapitate once and apply I.A.A. 1½ hours after decapitation.

III

It apparently needs no special experiments to ascertain that illumination of the test plants with orange or red light will influence likewise the results of the straight-growth (cylinder) test.

IV

It seemed worth while to know how long after the illumination the influence of orange light persists. In chapter II we showed that irradiation with orange light enhances the maximum of the first positive curvature. To solve the question indicated above, we irradiated coleoptiles unilaterally with 20 ergs $\lambda = 480$ mμ 0, 1, 2, 4 or 6 hours after a pre-illumination with orange light. From table XXIX it appears that the influence of orange light is still recognizable six hours after its application.

TABLE XXIX

Interval between pre-illumination with orange light and irradiation with blue light	Phototropic curvature in degrees after 20 ergs/cm² $\lambda = 480$ mμ	
	pre-illuminated coleoptiles	not pre-illuminated coleoptiles
0 hour	32 ± 1 (7)	15 ± 1 (5)
1 hour	21 ± 3 (5)	12 ± 2 (7)
2 hours	19 ± 2 (7)	14 ± 1 (7)
4 hours	19 ± 2 (5)	13 ± 2 (4)
6 hours	16 ± 0 (5)	12 ± 1 (5)

SUMMARY

1. Orange light, as used in the air-conditioned dark rooms, influences the reactions of Avena coleoptiles to indole-3-acetic acid (I.A.A.).

2. The orange light does not act upon the coleoptile directly, but through the intermediary of the tip of the primary leaf.

3. Light of $\lambda = 660$ mμ as well as light of $\lambda = 740$ mμ appeared to be active.

4. Irradiation of the Avena seedling as a whole, with 700 ergs/cm^2 $\lambda = 660$ mμ has two effects:

   a. it reduces the I.A.A. content of the coleoptiles.
   b. it enhances either the amount or the effect of an unidentified substance, here called the red light factor (R.L.F.).

5. The R.L.F. regulates the growth of the coleoptile in a narrow range of I.A.A. concentrations. It enhances the growth rate at low I.A.A. concentrations. In this way the one-peaked curve which presents growth as a function of the I.A.A. concentration is transformed into a two-peaked one.

6. Irradiation with 6000 ergs/cm^2 $\lambda = 740$ mμ annihilates effect 4b of light of $\lambda = 660$ mμ, but reduces, like the latter, the I.A.A. content of the coleoptile.

7. An explanation of the negative and of the second positive curvature could be based on a further study of the interaction of the R.L.F. with I.A.A.

8. The results of our experiments are a warning that the influence of orange and red light on the results of growth-substances tests should not be underestimated.

ACKNOWLEDGEMENT

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REFERENCES

Arisz, W. H. 1915. Rec. trav. bot. néerl. **12**: 44.
Avery, G. S.,P. R. Burckholder and H. B. Creighton. 1937. Bot. Gaz. **99**: 125.
Barlow, H. W. B., C. R. Hancock and H. J. Lacey. 1957. Ann. Bot. *N.S.* **21**: 257.
Beijer, A. 1927. Planta **4**: 411.
Blaauw, A. H. 1909. Rec. trav. bot. néerl. **5**: 209.
Brian, P. W. and H. G. Hemming. 1957. Nature **179**: 417.
——— and ———. 1958. Ann. Bot. *N.S.* **22**: 1.
Goodwin, R. H. and O. V. H. Owens. 1948. Bull. Torr. Bot. Cl. **75**: 18.
Hillman, W. S. and A. W. Galston. 1957. Plant Phys. **32**: 129.
Koningsberger, V. J. 1922. Rec. trav. bot. néerl. **19**: 1.
Lint, P. J. A. L. de. 1957. Meded. Landb. Hogeschool Wageningen **57**: 1.
Liverman, J. L. and J. Bonner. 1953. Proc. Nat. Ac. Sci. **39**: 905.
Oppenoorth, W. F. F. 1941. Thesis Utrecht.
Overbeek, J. van. 1936. Rec. trav. bot. néerl. **33**: 333.
———, D. W. Racusen, M. Tagami and W. Hughes. 1957. Plant. Phys. **32** suppl. XXXII.
Raalte, M. H. van. 1937. Rec. trav. bot. néerl. **34**: 279.
Roberts, D. W. A. 1951. Can. Journ. Bot. **29**: 451.
Schneider, C. L. 1941. Am. J. Bot. **28**: 878.
Schrank, A. R. 1950. Ann. Rev. of Plant. Phys. **1**: 59.
Terpstra, W. 1953. Thesis Utrecht.
Vogt, E. 1915. Z. f. Bot. **7**: 193.
Weintraub, R. L. and L. Price. 1947. Smith Misc. Coll. **105**: 1.
Went, F. W. 1956. A. Hollaender, Radiation Biology (New York Toronto London).
Wey, H. G. van der. 1931. Proc. Acad. Sci. Amst. **39**: Nr. 6.
Zollikofer, C. 1920. Proc. Acad. Sci. Amst. **23**: 1.

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DE LEVENSCYCLUS VAN CATAPODIUM MARINUM (L.) HUBBARD

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(*ingekomen 13 november 1958*)

Catapodium marinum (L.) Hubbard) werd in Nederland voor het eerst gevonden door Schoute en ter Pelkwijk aan de binnenrand van de Slufter op Texel in juni 1937. Twee jaar later, in juni 1939 vond Westhoff aan de Dellewal op Terschelling een viertal plantjes van dit gras. De derde groeiplaats in Nederland werd door mij op 27 mei 1952 ontdekt in de geïnundeerde Zwarte polder in Zeeuws Vlaanderen.

De volgende jaren bleek mij, dat het gras over een grote oppervlakte verspreid in de Zwarte polder groeide, meestal in forse, gedrongen, flink uitgestoelde, liggende planten, met ertussen steeds rechtopgroeiende, éénstengelige plantjes. Dit wekte bij mij het vermoeden, dat deze eenjarige soort gewoonlijk in het najaar kiemt en de winter doorkomt als jonge plant maar dat wellicht enkele zaden eerst in het voorjaar kiemen en deze dan de kleine plantjes met één stengeltje leveren. De vraag hoe kieming en groei van dit gras hier, aan de Noordgrens van zijn areaal verlopen, interesseerde mij, vooral toen in 1956, na de zeer strenge winter van 1955/56 niet anders dan de beschreven kleine, éénstengelige plantjes werden gevonden. De gevallen sneeuw was in de Zwarte polder ras verstoven en het gras was dus aan de felle koude en snijdende wind blootgesteld geweest. Blijkbaar hadden de planten deze koude niet overleefd en waren de gevonden exemplaren afkomstig van in het voorjaar gekiemde zaden.

Ik besloot toen, teneinde omtrent mijn veronderstelling zekerheid te krijgen, de ontwikkelingsgang van zaad tot bloeiende plant zo mogelijk in verschillende stadia te observeren. Ik koos hiertoe een gedeelte van het terrein, dat ten volle aan invloeden van weer en water was blootgesteld en waarvan de plantengroei het best met het door Westhoff c.s. beschreven Saginetum maritimae overeen kwam.

Op 25 mei 1956 deed ik mijn eerste waarnemingen. Nog slechts weinig plantjes vertoonden een begin van bloei, alle waren zeer klein, niet uitgestoeld en éénstengelig met weinig aartjes. Bijna alle grotere planten schenen op de groeiplaatsen doodgevroren of door zon en wind doodgebrand. Op 9 juni bezocht ik de groeiplaatsen weer; het had intussen flink geregend en de temperatuur was aanmerkelijk hoger. Alle plantjes waren volop in bloei, zij waren wat gerekt en veel groener, doch het bleef bij één stengeltje. Zij groeiden tezamen met kleine exemplaren van *Parapholis strigosa* (Dum.)

Hubbard, *Sagina maritima* G.Don, *Plantago coronopus* L., *Armeria maritima* Willd. en *Festuca rubra* L. Het geheel vormde een zeer armoedig gezelschap.

Op 12 juli waren de meeste plantjes afgestorven en hadden het zaad laten vallen. Zij waren echter voor mij, die de groeiplaatsen kende, nog goed herkenbaar. Teneinde het verdere verloop goed te kunnen volgen had ik enkele plaatsen van merktekens voorzien. Enkele plantjes waren na flinke regenval opnieuw gaan groeien en hadden lager aan het stengeltje, waarvan de top al vergaan was, een nieuw ontsproten, nog groene en bloeiende aar. Om zeker te zijn, dat ik de kieming van het zaad goed zou kunnen volgen, heb ik op die plaatsen enkele stengeltjes met aartjes oppervlakkig ingegraven. Op 16 augustus was alles volledig afgestorven en van enkele halmen, die ik weer opgroef, was het zaad nog niet gekiemd.

Bij een volgend bezoek, op 31 augustus, waren op de gemerkte plaatsen kleine kiemplantjes met ten hoogste vier zeer dunne sprietjes aanwezig. Bij het weer opgraven stelde ik door de aanwezigheid van de oude kafjes aan de kiemplantjes vast, dat zij inderdaad van *Catapodium marinum* waren en toen dat eenmaal was gebleken, kon ik ook op niet gemerkte plaatsen de kleine kiemplanten van die van andere grassen onderscheiden. Het ingraven bleek voor de kieming niet noodzakelijk te zijn geweest, want overal groeiden de kleine, goed ontwikkelde plantjes in goede gezondheid (Fig. 1a).

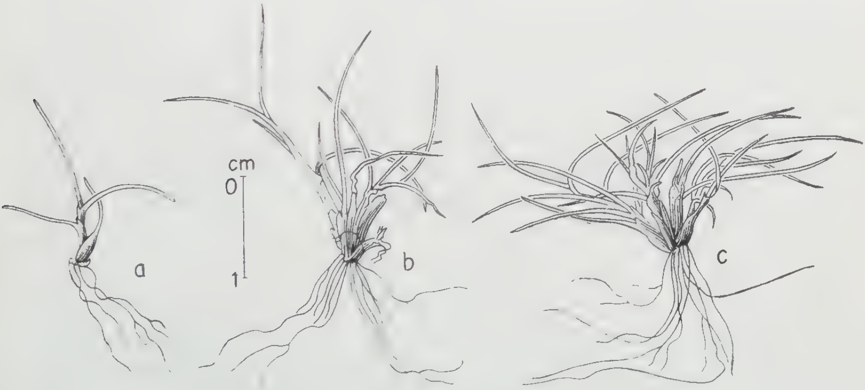

Fig. 1. Kiemplanten van *Catopodium marinum* (L.) Hubbard, Zwarte Polder. a. 31 augustus 1956; b. 30 october 1956; c. 26 november 1956.

Op 30 october waren de plantjes flink gegroeid en was een begin van uitstoeling waar te nemen (Fig. 1b).

De laatste maal dat ik in dit jaar de groeiplaats bezocht, was op 26 november. De kiemplanten leken nu volledig uitgestoeld, sommige hadden tot 12 spruiten; dat is ook het maximum aantal bloeiende stengels, dat ik in voorgaande jaren aan één plant had aangetroffen (Fig. 1c). Dit beloofde dus voor het volgende jaar bij niet te strenge winter weer grote vertakte planten.

Op 9 januari 1957 bleken de planten in rust te zijn. Ze waren sedert november niet meer gegroeid. Blijkbaar waren zij in het overwinteringsstadium. De winter verliep zonder veel koude en begin maart kon opnieuw groei worden geconstateerd. Omstreeks half april begonnen de bloeistengeltjes uit te schieten. Door koude vochtigheid duurde het evenwel toch nog tot 11 juni voor de planten volledig in bloei waren. Ze waren flink vertakt, doch door het ongunstige weer groeiden zij toch niet uit tot de forse exemplaren, die ik vóór 1956 verzameld had. Sporadisch trof ik tussen de vertakte planten weer éénstengelige exemplaren als voorjaarszaailingen aan.

Het onderzoek over 1957/58 verliep op ongeveer gelijke wijze. Ook de afgelopen winter bracht niet zodanige vorst of snijdende wind, dat de jonge planten te gronde gingen. Door het gunstige voorjaar groeiden de planten flink uit en zij waren overal in groot aantal, zowel op de beschreven plaatsen als tussen de hogere begroeiing aanwezig. Op de laatstgenoemde plaatsen schoten zij ijler op, waren niet zo sterk vertakt, doch langer. Door het zeer zonnige weer gedurende meerdere dagen in de bloeitijd werden de planten zeer rood en deden zij haar Nederlandse naam van "Laksteeltje" alle eer aan.

Op grond van dit onderzoek kan worden aangenomen, dat *Catapodium marinum* (L.) Hubbard op deze breedte in het najaar kiemt en als jonge plant overwintert. Zij komt de normale winters zonder schade door en na bevriezing bij strenge koude is er blijkbaar nog een klein gedeelte zaad voor voorjaarskieming beschikbaar, zodat het voortbestaan ook door winters met uitermate lage temperaturen niet wordt bedreigd.

De groeiplaats aan de Dellewal op Terschelling is in de oorlog als gevolg van vergraving door de bezetter verloren gegaan. In de Zwarte polder en in de Slufter groeit het gras thans nog in vrij grote hoeveelheden en het laat zich aanzien, dat zolang deze gebieden in hun tegenwoordige staat blijven, er voor verdwijnen van het gras geen vrees behoeft te bestaan.

SUMMARY

Catapodium marinum (L.) Hubbard is found growing in the Netherlands in the Slufter on the isle of Texel and in the inundated (flooded) Zwarte polder in Zeeuws Vlaanderen. An investigation was made on how the grass, that grows in the Netherlands on the northern boundary of its area, maintains itself. To that purpose a part of the habitat in the Zwarte polder was provided with marks. On these spots the development of the seed into the flowering plant was observed for the period of two years. It appeared that normally the seed germinates in the months of August/September and that the young plants have grown to thoroughly stooled plants before the setting in of the winter; in this stage they are able to hibernate when the winter is not too severe. A small percentage of the seed germinates not before spring, and the plants originated from this seed as a rule have only one flowering stem with few, small spikelets.

After the severe winter of 1955/56 on the marked spots one-stemmed plants were found exclusively, from which fact it may be concluded that the plants of the preceding autumn had not outlived the severe cold.

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NOTES ON AMERICAN GESNERIACEAE

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When studying the *Gesneriaceae* of Guiana (1958) the present author saw a fairly considerable number of misidentified and unnamed specimens some of which proved to belong to undescribed species. Several of the latter are described below. Besides, several of the species he met with, had to be transferred to other genera. New combinations, however, were made only in those cases where the author could examine the type.

Alloplectus

Section **Macrochlamys** (Dcne.) Fritsch in Engl. Prantl, Nat. Pflanzenf. 4(3b): 168. 1894 ("1895") (*Macrochlamys* Dcne., Rev. Hortic. Sér. 3. 3: 243. 1849, as genus).

Type species: *A. coccineus* (Aubl.) Mart. ex G.Don (*Macrochlamys patrisii* (D.C.) Dcne.).

Heterotypic synonym: *Erythranthus* (Oerst.) Hanst., Linnaea 34: 362. 1865 (*Erythranthus* Oerst., Centralamer. Gesn. 46. 1858, as genus). Type species: *A. coriaceus* (Oerst.) Hanst.

Leafblades oblong-elliptic, acuminate, entire or obscurely denticulate near the apex, on both sides either sparsely strigillose, or sparsely pubescent, or glabrous. Inflorescence axillary, 1- to several-flowered, usually with large, mostly purple or dark red bracts. Sepals coloured like the bracts, mostly large. Corolla mostly yellow, sometimes creamy or red, usually nearly cylindric; limb subactinomorphic. Anthers oblong, usually sagittate at the base. Capsule often yellow, bivalved, with a thickened ring along the line of dehiscence.

Two new species are described below. The way in which they differ from their nearest allies, may be seen from the following key.

1. Peduncle about as long as the leaves or longer. Peru . . . . **A. pendulus** Poepp. et Endl.
   Peduncle shorter than the leaves 2
2. Corolla red, 1.6–2.8 cm long; anthers 3 mm long. Panama, Costa Rica. . . . . **A. coriaceus** (Oerst.) Hanst.
   Corolla yellow or creamy, usually 3 cm long or more; anthers 5–8 mm long 3

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3. Inflorescence with large bracts covering the calyx; sepals often narrowed, never widened at the base 4
   Inflorescence without or with small bracts; sepals widened and subcordate at the base 7
4. Corolla about 4 times as long as the calyx, puberulous outside, about 4 cm long; sepals very small, about 1 × 0.3 mm, oblong-elliptic. PERU, COLOMBIA (?) . . **A. affinis** Mansf.
   Corolla 1–2 times as long as the calyx, puberulous or villose outside, 2.5–6 cm long; sepals obovate if less than 1.5 cm long 5
5. Outer bracts orbicular; sepals obovate, obtuse or rounded at the apex 6
   Outer bracts ovate or oblong-ovate; sepals oblong or oblong-ovate, acute or obtuse at the apex. BOLIVIA . . . . **A. doratostylus, sp. nov.**
6. Bracts and sepals puberulous; corolla villose-hirsute outside; limb small, red. PERU . . . . **A. erythroloma, sp. nov.**
   Bracts and sepals sparsely appressed-pubescent; corolla puberulous to villose outside, brown-purple- or reddish-brown-spotted in the throat or on the limb or not; limb conspicuous. COLOMBIA, southern VENEZUELA, GUIANA, northern BRAZIL . **A. coccineus** (Aubl.) Mart. ex. G. Don
7. Disk gland one, entire, 2- or 3-lobed. ECUADOR, PERU, BRAZIL . . . . **A. semicordatus** Poepp. et Endl.
   Disk glands three. ECUADOR . . . . **Crantzia pseudocordata** Cuatrec.

As the structure of the disk is the only character by which the two last-named species differ, and as their specific distinctness therefore is open to doubt, for **Crantzia pseudocordata** no new combination is proposed. Its type could not be sent on loan, and on a photograph of the latter the flowers were not visible.

Many species of this section are still undescribed.

A. doratostylus Lwbg., sp. nov. **Fig. Ad, p. 46**

Misapplied name: *A. patrisii* Rusby, Mem. Torr. Bot. Cl. 6: 97. 1896, not DC. (applies to the type collection).

Planta habitu *A. coccinei.* Folia cuiusque jugi aequalia vel subaequalia petiolata laminis oblique oblongo-ellipticis. Inflorescentia axillaris racemosa bracteis magnis coloratis sepala superantibus instructa. Sepala oblonga vel oblongo-ovata.

Corolla extus flava basi calcarata limbo patente. Stamina quattuor didynama inclusa filamentis apice contortis. Antherae oblongae basi sagittatae. Ovarium superum ovoideum. Stylus inclusus crassus apice incrassatus deciduus. Stigma bilobum. Disci glandula singula dorsalis magna emarginata glabra. Placentae facie interiore solum ovuliferae. Capsula subglobosa bivalvis. Semina fusiformia.

Type: BOLIVIA: Cochabamba, Espiritu Santo, vic. of Cochabamba, Bang 1259 (W, holotype, photograph in U; isotypes: BM, F, G: 2 sheets, K, M, MO, PH, US).

Epiphytic or terrestrial shrub, subshrub, or vine, about 2–3 m high. *Stems* sarmentose, branched or not, sometimes with spreading adventitious roots, puberulous at the apex, glabrous and shining. *Leaves:* petiole sparingly appressed-pubescent, 0.5–4 cm long; blade dark green above, beneath paler green, with purple or dark red veins (?) and often partially purple, 1¾–3½ (mostly 2–3) times as long as wide, 4–21 × 2–9 cm (mostly about 8–15 × 3–6 cm), fleshy, papyraceous or subcoriaceous when dry, acuminate at the apex, cuneate to almost decurrent at the base, entire or sometimes obscurely denticulate near the apex, sparsely appressed-pubescent to glabrous on both sides; primary veins 4–9 pairs, arcuate towards the margin. *Inflorescence* several-flowered. Peduncle very short, sparsely appressed-pubescent, 3–7 mm long. Bracts dark red or purple, leafy, veined, ovate or oblong-ovate, 1½–2 times as long as wide, 19–40 × 9–25 mm, acute or obtuse at the apex, rounded at the base, entire or sinuate, sparsely appressed-pubescent on both sides, the outer ones larger than the others, similarly shaped. Pedicels sparsely appressed-pubescent, 3–12 mm long. *Sepals* dark red or purple, free, veined, 2–3 × as long as wide, acute or obtuse at the apex, approximately rounded at the base, sinuate or obscurely serrulate, sparsely appressed-pubescent on both sides, four subequal, 19–29 × 7–14 mm, the fifth (dorsal) about half as long as the others or somewhat more, 13–15 × 5 mm. *Corolla* inside partially crimson in the throat and on the limb, especially dorsally, tubular, horizontal in the calyx, 1½–2 times as long as the calyx, 35–51 mm long, at the base 4–5 mm, at the throat 6–10 mm wide, contracted above the spur and in the throat, dorsally ventricose and there 8–11 mm wide, slightly bent upwards, puberulous outside, especially above, inside minutely puberulous near the insertion of the stamens: spur subglobose, 5–6 mm in diam.; tube 25–40 mm long; limb 8–13 mm wide; lobes subequal, rounded, obscurely crenate-serrate, 2.5–4 mm in diam. Filaments glabrous, widened at the base, all connate at the base, inserted on the base of the corolla; anthers violet on one side and white at the other (*teste* Steinbach), mostly connivent, free, 5–6 × 2 mm; cells discrete, dehiscent by a longitudinal split, which starts at the base. Staminode one, small, filiform, glabrous, inserted at the very base of the corolla, curved through the spur, 2 mm long, without anther. Ovary appressed-pubescent, 6 × 4.5 mm; style red, sparsely pubescent, 2–3 cm long. Stigma conspicuously paler than the style, yellow (?), pubescent with glandular hairs on both sides. Disk gland 1.5 mm high. Capsule yellow (*teste* Steinbach 5555), sparsely appressed-pubescent, 15–17 × 12–14 mm, with a thickened ring along the line of dehiscence, obtuse at the apex; valves coriaceous. Seeds reddish (?), shining, about 4 (3–6) times as long as wide, 1–1.2 × 0.2–0.3 mm, longitudinally striate.

Ecology: In rain forests; alt. 400–1400 m.

Distribution: Bolivia.

Paratypes:

BOLIVIA: LA PAZ: Mapiri Region, San Carlos, along road to San José, Buchtien 1349 (US); Charopampa, Mapiri, Buchtien 1973 (US).

BENI: vic. of Rurrenabaque, Cardenas 1669 (K); ibid., Reyes Region, Beni R., Fleischmann 270 (S).

COCHABAMBA: prov. Chapare, along road to Todos Santos, near Chimore, Eyerdam 24832 (UC, G); vic. of Espiritu Santo, vic. of Cochabamba, Buchtien 3107 (NY); R. Juntas, herb. Kuntze s.n. (US).

SANTA CRUZ: prov. Sara, Bosque del Fraile, Steinbach 7494 (BM, G, K, S, U); prov. Sara, Bosques del R. Surutu, Buena Vista, Steinbach 5555 (A, F); Plaja-Ancha, Upper R. Ichilo-Vallegrande, Cardenas 4045 (F, US).

Sine loco: Bang 2540 (NY, US).

Etymology: *δόϱυ, δόϱατος*, lance referring to the lance-shaped style.

A. erythroloma Lwbg., sp. nov. **Fig. Ae, p. 46**

Misapplied name: *A. circinatus* Poepp. et Endl., Nov. Gen. 3: 5. 1845, not Mart.; see also Hanstein, Linnaea 34: 365. 1865, who cites Spruce 4608, and who had also seen the specimen of Poeppig, no. 2230.

Planta habitu *A. coccinei*. Folia cuiusque jugi subaequalia vel inaequalia petiolata laminis ellipticis vel oblongo-ellipticis. Inflorescentia axillaris racemosa bracteis magnis coloratis instructa. Sepala oblongo-obovata. Corolla flava limbo coccineo patente. Stamina quattuor didynama inclusa filamentis apice contortis. Antherae oblongae basi sagittatae. Ovarium superum ovoideum. Stylus inclusus apice incrassatus. Stigma bilobum. Disci glandula singula dorsalis magna integra glabra. Placentae facie interiore solum ovuliferae. Capsula subglobosa bivalvis. Semina fusiformia.

Type: Peru: Loreto, Balsapuerto, Klug 2965 (G, holotype, photograph in U; isotypes: BM, F, GH, K, S, US).

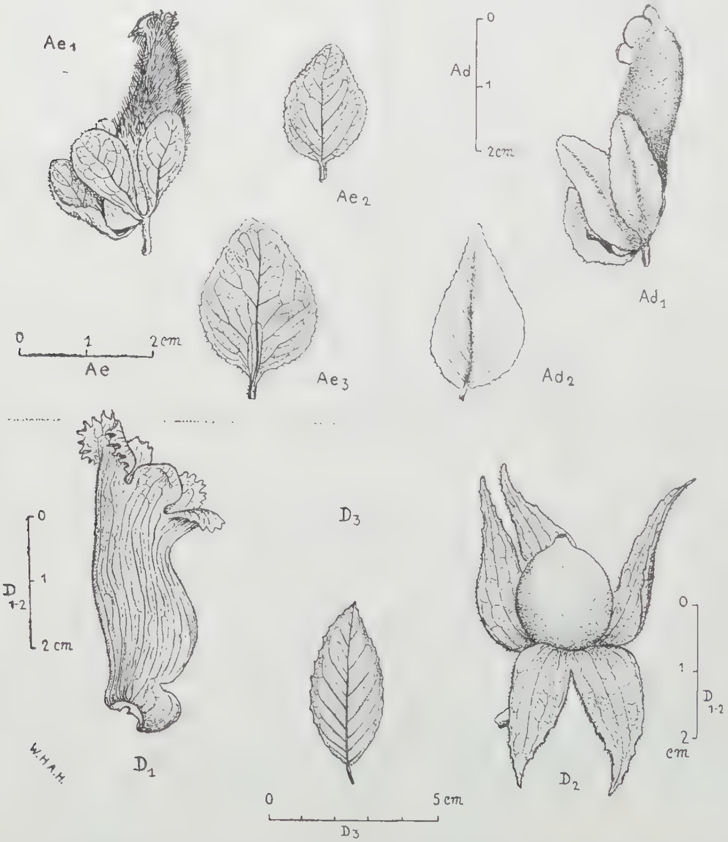

Fig. Ad. *Alloplectus doratostylus:* 1. flower (Steinbach 5555); 2. bract (Bang 2540); Fig. Ae. *A. erythroloma:* 1. flower; 2 and 3. bracts (1-3, Klug 2965); Fig. D. *Drymonia oxysepala:* 1. corolla (Klug 4281); 2. calyx with fruit (Ule 6574); 3. leaf (Klug 2965).

Terrestrial or epiphytic shrub, or vine, 0.60–1.50 m high or more (?). *Stems* sarmentose, branched or not, sometimes with spreading adventitious roots, puberulous at the apex, sparsely and often minutely pubescent and shining. *Leaves:* petiole sparsely appressed-pubescent to glabrous, 7–85 mm long; blade dark green above, beneath paler green with purple or dark red veins or entirely dark red or purple (?), 2–3 times as long as wide, variable in size, 8–30 × 3.5–13 cm, coriaceous also when dry, acuminate at the apex, rounded or cuneate to almost decurrent at the base, entire, sparsely appressed-pubescent to glabrous on both sides; primary veins 5–9 pairs, curved along the margin. *Inflorescence* several-flowered. Peduncle very short, puberulous, 3–7 mm long. Bracts dark red or purple, leafy, veined, rounded, ovate, or oblong-ovate, 1–2 × as long as wide, 20–28 × 11–26 mm, acute, obtuse, or acuminate at the apex, cuneate, rounded, or subcordate at the base, entire or obscurely serrulate, puberulous on both sides, outer ones rounded or nearly so, mostly larger than the others. Pedicels puberulous, 5–7 mm long. *Sepals* dark red or purple, free, veined, about 2 times as long as wide, 12–19 × 6–10 mm, obtuse or rounded at the apex, cuneate at the base, obscurely crenate-serrate, puberulous on both sides. *Corolla* tubular, about 2 times as long as the calyx, 25–35 mm long, at the base 3–4 mm, at the throat 4–6 mm wide, spurred at the base, contracted above the spur and in the throat, slightly ventricose in the middle and there 7–10 mm wide, slightly bent upwards, densely villose-hirsute outside, inside, especially near the insertion of the stamens, minutely puberulous with glandular hairs; spur obtuse; tube 17–25 mm long; limb small, 6–9 mm wide; lobes subequal, rounded, obscurely crenate-serrate, 3–4 mm in diam. Filaments glabrous, widened and connate at the base, inserted at the base of the corolla; anthers connivent, free, 5 × 1.5 mm; cells discrete, dehiscent by a longitudinal split which starts at the base. Staminode one, small, filiform, glabrous, inserted at the very base of the corolla, curved through the spur, 2.5 mm long, without anther. Ovary softly hirsute, 5–6 × 3.5 mm; style red, sparsely pubescent, about 2 cm long; stigma conspicuously paler than the style, yellow (?), pubescent with glandular hairs on both sides. Disk gland 1.5–2.5 mm high. Capsule sparsely pubescent, 12–15 × 11–13 mm. Seeds dark (?) brown, shining, about 3 times as long as wide, 1.2–1.5 × 0.3–0.5 mm, longitudinally or slightly obliquely striate.

Ecology: In rain forests, at low elevations.

Distribution: Peru.

Paratypes:

Peru: Loreto: Puerto Arturo, Lower R. Huallaga, below Yurimaguas, alt. about 135 m, Killip & Smith 27740 (US); Yurimaguas, Lower R. Huallaga, alt. about 135 m, Killip & Smith 28068 (US); ibid., Ule 6278 (G, HBG, L); Maynas, near Yurimaguas, Poeppig 2230 (W).

San Martín: near Tarapoto, Spruce 4608 (BM, BR, CGE, K, 3 sheets).

Etymology: ἐρυθρός, red; λῶμα, limb; the corolla limb is dark red.

A. semicordatus Poepp. et Endl., Nov. Gen. 3: 5. 1845; Hanstein, Linnaea 34: 364. 1865.

Type: Peru: Loreto, Cochero, Poeppig 1038 (W, holotype, photographs in F, U, and US; isotypes: LE, W).

Homotypic synonym: *Crantzia semicordata* (Poepp. et Endl.) Fritsch in Engl. Prantl, Nat. Pflanzenf. 4 (3b): 168. 1894 ("1895"); in Engl., Bot. Jahrb. 37: 486. 1906.

Heterotypic synonym: *Alloplectus sylvarum* S. Moore, Trans. Linn. Soc. Ser. 2. 4: 411. 1895. Type: Brazil: Matto Grosso, between Santa Cruz (Barra do Bugres) and Tapirapuan, S. Moore 390 (BM).

As this species has been interpreted in different ways, a new and more detailed description seems to be desirable.

Flowers axillary, solitary or in few-flowered short-pedunculate inflorescences without or with some sepal-like bracts which are often very small. Sepals dark red or purple, large, leafy, veined, ovate, 1½–2 times as long as wide, acuminate at the apex, subcordate at the base, sinuate or obscurely and remotely serrulate, sparingly appressed-pubescent on both sides, four subequal, 20–38 × 12–24 mm, the fifth (dorsal) one-third to two-thirds of the length of the others. Corolla (resembling that of *A. coccineus*) yellow, inside sometimes suffused with red, puberulous outside; limb spreading.

Terrestrial or epiphytic shrub, subshrub, or vine, 0.60–3 m high. *Stems* sarmentose, branched or not, sometimes with spreading adventitious roots, puberulous at the apex, practically glabrous and shining. *Leaves* of a pair unequal, petiolate, the larger one mostly 2–2½ times as long as the other; petiole sparsely appressed-pubescent to glabrous, 3–55 mm long; blade dark green above, beneath paler green with purple or dark red veins (?) or reddish, oblong-elliptic, 2–4 (mostly about 3) times as long as wide, 3–25 × 1.5–10 cm, papyraceous when dry, acuminate at the apex, rounded or cuneate to almost decurrent at the base, entire, sparingly strigillose to glabrous on both sides; primary veins 4–9 pairs, arcuate towards the margin. *Inflorescence:* peduncle very short or obsolete, 2–5 mm long, appressed-pubescent. Pedicels appressed-pubescent, 4–17 mm long. *Corolla* tubular, 1–1¾ × as long as the calyx, 35–60 mm long, at the base 4–8 mm, at the throat 6–12 mm wide, spurred at the base, contracted above the spur and in the throat, ventricose in the middle and there 10–13 mm wide, inside near the insertion of the stamens and dorsally in the throat minutely pubescent; spur subglobose; tube 25–40 mm long; limb 12–24 mm wide; lobes subequal, rounded, obscurely crenate-serrate, 5–15 mm in diam. Stamens 4, didynamous, included; filaments glabrous, widened at the base, contorted at the apex, all connate at the base, inserted at the base of the corolla; anthers connivent, free, oblong, 6–7 × 2 mm, sagittate at the base; cells discrete, dehiscent by a longitudinal split starting at the base. Staminode one, very small, glabrous, 0.6 mm long, acuminate. Ovary appressed-pubescent (not glabrous!), ovoid, 5–6 × 3–3.5 mm; style red, included, thick, sparsely pubescent, thickened at the apex, deciduous; stigma conspicuously paler coloured than the style, yellow (?), bilobed, pubescent with glandular hairs on both sides. Disk gland one, dorsal, large, either entire, 2-, or 3-lobed, glabrous. Placentae ovuliferous on the inner surface only. Capsule yellow, white, or brown-purple (*teste* Poppig), subglobose, sparsely appressed-pubescent, 16–19 × 13–15 mm, bivalved, with a thickened ring along the line of dehiscence, obtuse at the apex; valves coriaceous. Seeds dark brown, shining, fusiform, about 4 times as long as wide, 1.2 × 0.3 mm, longitudinally or slightly obliquely striate.

Ecology: Erect, creeping, climbing, or scrambling over shrubs, in rain forests; alt. 100–1540 m.

Distribution: Ecuador, Peru, and the adjacent part of Brazil.

ECUADOR: prov. Napo-Pastaza, Canton Napo, Zatzayacu, Mexia 7065 (UC, US); Gualaquiza, Pearce 238 (K).

PERU: LORETO: Gamitana Cocha, R. Mazán, Schunke 202 (F, GH, NY, UC); Iquitos, Ll. Williams 8194 (US); Mishuyacu, near Iquitos, Klug 120 (US); San Antonio, on R. Itaya, Killip & Smith 29491 (US); between Yurimaguas and Balsapuerto, Killip & Smith 28086 (US), 28138 (US); Santa Rosa, lower R. Huallaga, below Yurimaguas, Killip & Smith 28770 (US), 28808 (US), basin of R. Ucayali, Tessmann 3197 (G); Pucallpa, R. Neshuiya, Sandeman 3470 (K); ibid., Velarde Nuñez 2467 (US), 2487 (US); Boqueron Padre Abad, Woytkowski 34361 (G, MO); Cochero, near Pampayaco, Poeppig 1038 (W, holotype, photographs in F, U. and US; isotypes: LE, W); R. Pangoa, Matthews 1207 (K).

SAN MARTÍN: Zepelacio, near Moyobamba, Klug 3558 (G, US); east of Tingo Maria, Allard 20413 (US).

HUÁNUCO: Ganso Azul, R. Pachitea, Sandeman 3410 (K); vic. of Tingo María, Naranjillo, Ferreyra 2204 (US); Isla Tingo María, Ferreyra 1930 (US); Cerro Azul, km 176 Huánuco to Pucallpa, Seibert 2263 (US); distr. Churubamba, Hacienda Mercedes, prov. Huánuco, Mexia 8182 (UC, F, GH), 8222 (UC, BM, F, MO, U, US).

Junín: Pichis Trail, San Nicolas, Killip & Smith 25985 (US), 26007 (US); Cahuapanas, on R. Pichis, Killip & Smith 26728 (US); Puerto Yessup, Killip & Smith 26257 (US); Puerto Bermudez, Killip & Smith 26422 (US).

Madre de dios: R. Acre, Seringal Auristella, Ule 9773 (G, K, L).

Dept.?: Casapi (?), Matthews 1999 (K); St. Gavan (?), Lechler 2471 (K).

Sine loco: Dombey s.n. (P, U); Ruiz & Pavon 18/51 ("*Besleria calydermos*") (MA).

Brazil: Amazonas: near mouth of R. Embira, trib. of R. Taraucá, Krukoff 5893 (G).

Acre: Juruá-Mirim, R. Jurua, Ule 5694 (G, HBG, K, L).

Matto Grosso: between Santa Cruz (Barra do Bugres) and Tapirapuan, S. Moore 390 (BM, type of *A. sylvarum*).

Chile: sine loco, herb. Richard s.n. (P) (very doubtfully from that country).

Besleria

B. delphinioides (Seem.) Lwbg., comb. nov.

Basionym: *Drymonia delphinioides* Seem., Voy H. M. S. Herald 186. 1854.

Type: Colombia: Chocó, Cabo Corrientes, Seemann 1054 (K, holotype).

This species belongs to *Besleria*, section *Neobesleria*, subsection *Herbaceae*, and is very closely related to *B. subcoriacea* Morton (Contrib. U.S. Nat. Herb. 29: 28. 1944). It is placed in *Besleria* by virtue of its anthers, which are reniform and all four coherent. It is perhaps not specifically different from *B. subcoriacea*, from which it differs only by the obtuse instead of rounded apex of the sepals and by the longer pedicel. In all other characters it agrees with Morton's description. It was collected not so far from the type locality of *B. subcoriacea*. The latter is Bahia Solano, which lies about 180 miles north of Cabo Corrientes.

Columnea

C. dimidiata (Benth.) Lwbg., comb. nov.

Basionym: *Alloplectus* (?) *dimidiatus* Benth., Pl. Hartweg. 235. 1846.

Type: Colombia: Cauca, Cordillera Occidental, vic. of Popayán, Hartweg 1266 (K, holotype, isotypes: CGE, 2 sheets, G. K, photographs of CGE sheets in U and WAG).

This species belongs to *Columnea* section *Collandra*, and is related to *C. guianensis*. It is placed there because of the following characters: Leaves of a pair strongly unequal, the larger one 4–6 times as long as the other, lanceolate, deep green above, red or partially red beneath, the smaller one stipulelike, ovate-lanceolate. Flowers axillary. Bracts large, leafy, acuminate. Corolla nearly cylindric, 4–5 cm long, contracted at the throat; tube red; limb yellow, erect; lobes small, subequal, rounded.

Additional specimens examined:

Colombia: Caldas: R. San Rafael, below Cerro Tatamá, Pennell 10411 (PH).

Tolima: Quindío, Dawe 799 (K), ibid. (?), Dawe 825 (K); ibid., Novilleros, André 2354 (K); Ibaque, Goudot 5 (P).

VALLE DEL CAUCA: Palmira, Cord. Centr., Killip 6152 (GH); San Antonio, Cord. Occ., Dryander 2299 (BM); La Cumbre, Cord. Occ., Killip 5589 (PH); ibid., Pennell 5155 (GH, K, PH).
CAUCA: near Cali, Lehmann 5850 (K), Sept. 1895 (K).

C. lanata (Seem.) Lwbg., comb. nov.

Basionym: *Alloplectus lanatus* Seem., Voy. H. M. S. Herald 186. 1854.

Type: COLOMBIA: Chocó, Cabo Corrientes, Seemann 1056 (K, holotype, photographs: U, WAG; isotypes: BM, GH, GOET).

This species too belongs to *Columnea*, section *Collandra*, and is allied to *C. guianensis* by the following characters: Leaves of a pair strongly unequal, the larger one about 12–15 times as long as the other, oblique, lanceolate, green above, with a red area beneath, the smaller one stipule-like, ovate-lanceolate. Flowers axillary. Bracts large, leafy, obtuse. Corolla cylindric, contracted in the throat, lanate-tomentose outside; limb erect; lobes small, subequal.

Drymonia

D. latisepala (Rusby) Lwbg., comb. nov.

Basionym: *Columnea latisepala* Rusby, Mem. Torr. Bot. Cl. 4: 239. 1895.

Type: BOLIVIA: Songo, Bang 869 (NY, holotype, not seen; isotypes: F, W!).

This species is related to *D. calcarata* Mart., the type species of the genus. It belongs to the section *Drymonia* and has its place there by virtue of the following characters: Sepals broadly ovate, large, hirsute on both sides. Corolla amply tubular, horizontal in the calyx, about 1.5 × as long as the calyx, hirsute outside; limb large, spreading; lobes rounded, the ventral one larger than the others, erose-fimbriate, the others serrate. Anthers oblong, sagittate at the base, similar to those of *D. calcarata*.

By the shape of the corolla lobes it resembles *D. serrulata*, from which it differs strikingly by its indumentum.

D. oxysepala Lwbg., sp. nov. **Fig. D, p. 46**

Planta terrestris vel epiphytica repens vel scandens. Folia petiolata laminis oblongo-ellipticis. Flores axillares. Sepala foliacea oblongo-ovata vel ovato-lanceolata apice longe acuminata basi rotundata. Corolla ample tubularis basi calcarata fauce non contracta extus puberula limbo patente. Stamina quattuor didynama inclusa filamentis glabris contortis basi omnibus inter se connatis et basi corollae insertis. Antherae conniventes liberae oblongae basi sagittatae. Ovarium superum. Stylus inclusus crassus brevis. Disci glandula dorsalis singula magna glabra integra. Placentae duae bilamellatae facie interiore solum ovuliferae. Capsula subglobosa bivalvis. Semina ellipsoidea.

Type: PERU: San Martín, Juan Jui, Alto R. Huallaga, Klug 4281 (U, holotype, isotypes: A, UC).

Herb, or vine, 0.30 m high or more (?). *Stems* sarmentose, branched or not, with spreading adventitious roots, puberulous and shining, glabrescent. *Leaves* of a pair equal or subequal; petiole puberulous, 2–10 mm long; blade dark green above, paler beneath, 1.5–3 (mostly 2–2.5) × as long as wide, 18–85 × 8–46 mm (mostly about 30–60 × 15–30 mm), papyraceous when dry, acute or acuminate at the apex, cuneate or rounded at the base, serrulate, puberulous on both sides; primary veins 4–7 pairs, arcuate towards the margin. *Flowers* solitary or 2–3 together. Peduncle obsolete or very short, often with some small bracts. Bracts linear, about 10 times as long as wide, 6–9 × 0.5–1 mm, long-acuminate, entire, puberulous on both sides. Pedicels puberulous, 6 mm long. *Sepals* brownish-green (*teste* Woytkowski 35223), connate at the base up to one-half of their length, 3–5 times as long as wide, 25–33 × 5–11 mm, remotely serrate, puberulous on both sides; four erect, oblique; the fifth (dorsal) curved around the spur. *Corolla* white outside, inside dark red- or purple-spotted in the throat and yellow downwards, fleshy, horizontal in the calyx, about 1.5–2 times as long as the calyx, 40–58 mm long, at the base 7–10 mm, at the throat 15–22 mm wide, contracted above the spur, dorsally ventricose and there 15–17 mm wide, inside partially pubescent with glandular hairs; tube 26–37 mm long; spur subglobose, 7–8 mm in diam.; limb slightly bilabiate; lobes unequal; the ventral one larger than the others, broadly rounded, about 1.5 × as wide as long, 7–11 × 11–16 mm; the four others equal, nearly rounded, 5 × 7 mm; the two lateral ones subentire or serrulate, and the two dorsal ones serrate. Filaments widened at the base. Anthers 6 × 2 mm; cells dehiscent by a longitudinal split starting at the base. Staminode none. Ovary appressed-pubescent, ovoid or subglobose, 6 × 4–5 mm; style puberulous; stigma bilobed (?). Capsule puberulous, 15–16 × 12–13 mm, with a thickened ring along the line of dehiscence, obtuse at the apex; valves thick, coriaceous. Seeds (immature?), medium brown, shining, about 3 times as long as wide, 0.8 × 0.25–0.3 mm, longitudinally or obliquely striate.

Description of fruit and seeds based on Ule 6574.

Ecology: In rain forests; alt. about 250–900 m.

PERU: SAN MARTÍN: prov. San Martín, near Tarapoto, Spruce 4240 (BR, K: 2 sheets, W); ibid., 4 miles east of Tarapoto, Woytkowski 35223 (UC, F); Juan Jui, Alto R. Huallaga, Klug 4281 (U, holotype, isotypes: A, UC).

LORETO: Boquerón Padre Abad, Woytkowski 34373 (UC, F); San Antonio de Compasso, Ule 6574 (HBG).

Episcia

E. ciliosa (Mart.) Hanst., Leeuwenberg, Acta Bot. Neerl. 7: 401. 1958.

Description of mature fruits (not previously available):

Capsule globose, bivalved, 4 mm in diam. Seeds dark brown, shining, ellipsoid, about 4 times as long as wide, 0.8–1 × 0.2–0.25 mm, longitudinally striate, obtuse at the apex, mucronate at the base, with long white diaphanous funiculi and with a small arillus (Maguire & Fanshawe 32368 (US).).

E. porphyrotricha Lwbg., Acta Bot. Neerl. 7: 311, 411. 1958.

This species has been based on two specimens from the mountains of British Guiana. The leaves of these specimens were not bullate, otherwise they could not have been pasted entirely to the sheets. Now it is also known from three localities in the Venezuelan part of the Guayana Highlands. The following characters taken from these specimens may serve to complete the description:

Leaves of a pair subequal, usually with shorter petioles than those of the type specimen, most of them crowded at the apex of the stem; petiole 5–40 (mostly about 10–20) mm long; blade above sometimes with a pale green area along the midrib (*teste* Steyermark & Wurdack 105), sometimes bullate. Pedicels up to 35 mm long. Corolla vermilion, crimson, or scarlet, trumpet-shaped or infundibuliform, 35–54 mm long, at the throat up to 9 mm wide, scarcely or not contracted in the throat; tube 28–42 mm long. Capsule globose, 6–9 mm in diam. Seeds dark brown, shining, ellipsoid, about 1½–2 × as long as wide, 0.5–0.8 × 0.3–0.4 mm, obliquely striate, with long white diaphanous funiculi and with a small arillus.

VENEZUELA: BOLÍVAR: Chimantá Massif, vic. of Techiné-Merú, along R. Aparurén, alt. 470 m, Steyermark 76045 (US); ibid., along R. Tirica, alt. 470 m, Steyermark & Wurdack 105 (US), 106 (US).

Episcia dariensis (Seem.) Lwbg., comb. nov.

Basionym: *Alloplectus dariensis* Seem., Voy. H. M. S. Herald 187. 1854; Hanstein, Linnaea 34: 424. 1865; Leeuwenberg, Acta Bot. Neerl. 7: 312. 1958.

Type: COLOMBIA: Chocó, Cabo Corrientes, Seemann 1058 (K, holotype, photographs in U and US; isotype: BM).

As mentioned in my previous paper, this species, like the two following ones, belongs to the section *Paradrymonia* of *Episcia*. The grounds for their transference are:

Stems very short, with spreading adventitious roots. Leaves apparently spreading (those of a pair strongly unequal and the smaller one soon deciduous (?) as in most species of this section); petiole about 4–11 cm long; blade lanceolate, about 3–5 times as long as the petiole, 4½–7 × as long as wide, 19–32 × 3–6 cm, acuminate at the apex, long-decurrent into the petiole, practically glabrous. Sepals dark red or purple, linear, fimbriate, about 2 cm long, glabrous or nearly so. Corolla yellow, infundibuliform, about 3–4.5 cm long, spurred at the base, sparsely and minutely pubescent outside; lobes entire or subentire (?). Anthers glabrous, coherent in pairs; cells parallel, discrete, dehiscent throughout by a longitudinal split.

Besides the type collection only known from the following localities: COLOMBIA: CHOCÓ: La Concepción, 15 km east of Quibdó, alt. about 75 m, Archer 1968 (US).

E. conferta (Morton) Lwbg., comb. nov.

Basionym: *Centrosolenia conferta* Morton, Journ. Wash. Acad. Sci. 35: 126. 1945.

Type: COLOMBIA: Antioquia, north of Dabeiba, along road to

Turbo, alt. 300–350 m, Metcalf & Cuatrecasas 30200 (UC, holotype, photographs in U and US; isotype: US).

Only known from the type collection.

E. decurrens (Morton) Lwbg., comb. nov.

Basionym: *Centrosolenia decurrens* Morton, Field Mus. Publ. Bot. 18: 1158. 1938.

Type: Costa Rica: Finca Montecristo, on the R. Reventazón below Cairo, prov. Limón, Standley & Valerio 48589 (US, holotype, photograph in U).

Leaves sparsely hirsute to glabrous above, hirsute beneath, especially along the midrib and veins, the younger ones entirely red-tomentose-hirsute. Capsule globose, 5–6 mm in diam., red-hirsutulous, bivalved. Seeds dark brown, shining, ellipsoid, about 4 times as long as wide, 1–1.2 × 0.25–0.3 mm, longitudinally striate with long brownish(?) funiculi and with a small arillus.

Ecology: on trees in rain forests; alt. 0–500 m.

A collection from Panama is now available:

Panama: vic. of Chiriquí Lagoon, prov. Bocas del Toro, von Wedel 2279 (US).

E. lineata (Morton) Lwbg., comb. nov.

Basionym: *Centrosolenia lineata* Morton, Ann. Mo. Bot. Gard. 29: 41. 1942.

Type: Panama: north of El Valle de Anton, Trail to la Mesa, alt. about 1000 m, Allen 2717 (US, holotype, photograph in U; isotype: MO).

The specimens enumerated below may belong to this species, but they differ from the type specimen by the following characters:

Sepals pilose instead of sparsely strigillose. Corolla purple-spotted on the limb (*teste* A. Smith) or pink-spotted (*teste* Brenes 4076) or with pink (*teste* Brenes 4412) instead of reddish-brown stripes.

Costa Rica: San Ramón, Brenes 3687 (F), 3949 (F), 4039 (F), 4076 (F), 4412 (F), 6117 (F); Quebrada Azul, San Carlos, prov. Alajuela, Brenes 23055 (NY); La Peña de Zarcero, Canton Aljaro Ruiz, prov. Alajuela, A. Smith H 1064 (F, US), H 1066 (F, US), NY 1066 (F, NY); San Luis de Zarcero, Canton Aljaro Ruiz, prov. Alajuela, A. Smith NY 1309 (F, NY); Quebrada Serena, southeast of Tilarán, prov. Guanacaste, Standley & Valerio 46284 (US, p.p.).

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NOTES ON MYRTACEAE VIII

TWO NEW SPECIES FROM AFRICA

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(*received November 27th, 1958*)

Syzygium Germainii Amshoff n.sp.

Arbor parva circ. 15 m alta ramulis robustis acute quadrangularibus omnino glabra. Folia petiolata, oblonga, basi truncata, late rotundata vel subcordata, apice acuta, 8–19 cm longa, 2–8 cm lata, coriacea, costa supra impressa, subtus crassa prominente, nervis lateralibus numerosis, utrinque prominulis. Petiolus canaliculatus, margine alatus, ½ 1½ cm longus. Inflorescentia terminalis, cymoso-paniculata, ramulis quadrangularibus articulatis robustis. Alabastra circ. 5 mm in diametro. Sepala late rotundata, 2 mm longa. Petala coalita, operculum circ. 5 mm in diametro formantia. Stamina 17 mm longa. Bacca ignota.

Belgian Congo, Boenda, Tshuapa, Germain 8347 fl. 16.5.1954, type (BR, duplicate in WAG.).

By its large leaves and relatively large flowers this species is, among the species of the Belgian Congo, most similar to *S. Giorgii* De Wildem. and *S. Gilletii* De Wildem.; it differs, however, from both species by its distinctly petiolate leaves and less dense inflorescence. Another species which may be compared is *S. Rowlandii* Sprague, with the leaves cuneate or acutish at the base.

Syzygium parvulum Mildbread ined. ex Amshoff.

Frutex glaber 4–6 m altus. Ramuli graciles, quadrangulares. Folia parva, petiolata, elliptica, basi acuta, apice obtusa vel brevissime obtuse acuminata, coriacea, glabra, 1½–3 cm longa, 1–1½ cm lata, costa supra impressa, subtus prominente; nervis lateralibus venisque fere obsoletis. Petiolus 4 mm longus, gracilis. Inflorescentia parva, terminalis. Flores albi, pro genere minimi; alabastra globosa, circ. 1 mm in diametro. Filamenta vix 2 mm longa. Bacca ignota.

Tanganyika Territory: Morogoro district, Uluguru mountains, N.W. side, 1900 m, Schlieben 3922 fl. 13–5–1933 (BR, ZU).

A mountain species very distinct by its small leaves and exceptionally small flowers.

BRIEF REPORTS

JANSSEN, C. R.: Alnus as a disturbing Factor in Pollen Diagrams

It is commonly accepted that percentages of pollen in a pollen diagram do not express the exact composition of forests in earlier times. This inaccuracy is due to several factors, for instance the different quantities of pollen produced by plants, the distance of transport etc. A pollen diagram tells us only the change in pollen rain on the locality where we collected soil samples. In studying a pollen diagram we find a close relation between the variations in the percentages of a certain species and the area occupied by this species in the vegetation. When the percentage of pollen of a species increases, we conclude generally that the relative area occupied by this species in the vegetation increases too. However, such a connection might be doubted. The variety of factors controlling the dispersion of pollen is so great that the interpretation of a pollen diagram often meets with great difficulties. The connection between pollen rain and the composition of the vegetation is a simple one in the cases where we are dealing with a region of uniform vegetation. A diagram taken from a region in which the vegetation varies from place to place has to be regarded with some caution. Unfortunately such a heterogenity of the vegetation exists on the very place, where we want to compose a pollen diagram.

The pollen rain which falls into a bog arises from two sources: a pollen rain from the local vegetation of the bog itself and one from the surrounding vegetation. When we are dealing with great bogs, the pollen produced by the vegetation of the bog itself will be mostly that of herbaceous plants, shrubs, and spores of the *Bryophyta* and the *Pteridophyta*. It is the rule rather than the exception that the bog will be treeless. The tree pollen in such a bog mostly takes its origin from the surrounding forests. It is a fortunate circumstance in a diagram that pollen of trees is separated from other pollen. However, one exception is seen in the way in which Iversen composes a diagram for late glacial times. This method, commonly used for late glacial times, embraces a pollen sum not only containing trees but also some herbaceous plants. The origin of the latter can, with some certainty, be accepted as from outside the bog. Therefore the local vegetation of the bog does not influence the percentages of tree pollen. The pollen sum thus comprises pollen of plants which grow under the same biotic conditions.

However, there exist diagrams the pollen sum of which contains pollen of tree species not growing under the same conditions. One of the tree species belonging to the bog itself may show pollen variations which are independent of the tree species outside the bog. These variations, therefore, are reality only for the species growing in the bog and should not be applied to those outside. By adding the pollen of this species to the pollen sum we have the disadvantage that the species strongly influences the percentages of other tree species. In order to interpret the history of the forests it will be necessary to remove such a tree from the tree-pollen sum. It will be clear that we must know with some certainty whether a tree belongs to the bog itself.

Indeed there are diagrams which show this phenomenon very clearly. Figure 1 gives a diagram from a bog in the southern part of the province of Limburg. The bog is situated at the bottom of the valley of the Geleen river near Nuth. The diagram shows very high percentages of *Alnus* (average about 80 %). It is not very difficult to explain these high percentages, because in the present the vegetation of the bog is an *Alnetum*. It is known that *Alnus* likes wet places and these very places are fairly rare in a hilly landscape like Limburg. *Alnus* does not occur on the surrounding slopes.

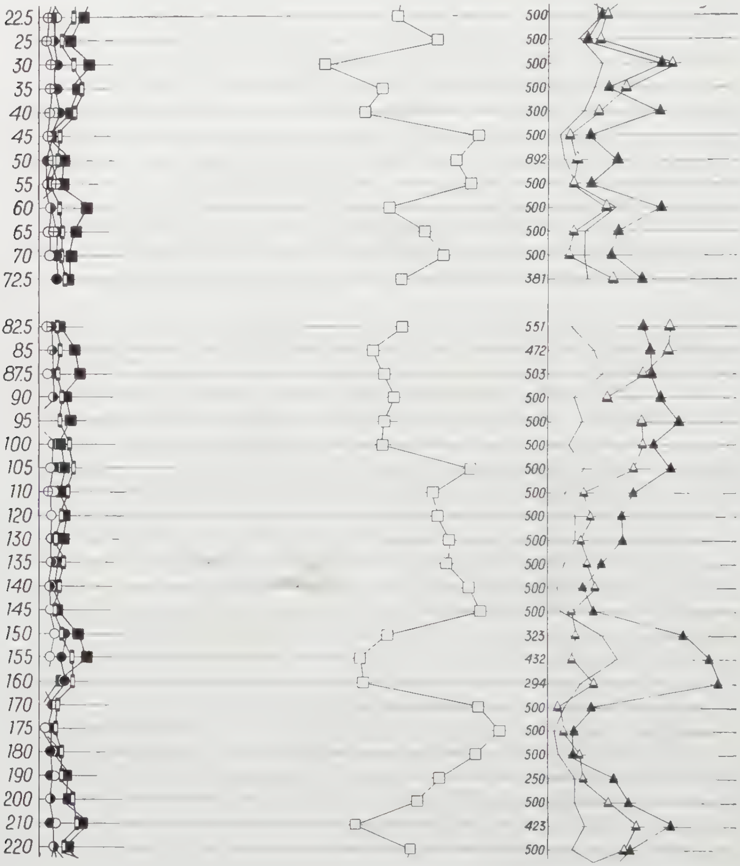

Fig. 1. Pollen diagram of Nuth, including *Alnus* in the tree-pollen sum.

The tree following *Alnus* in importance in the diagram is *Fagus*, a tree which grows only on the drier slopes. In the diagram we notice little maxima of *Fagus* on depths of 60, 95, 160 and 210 cm. However on the same depths *Alnus* shows a slight decrease. Therefore it may be said that the maxima of *Fagus* are artifacts, caused by a local decrease of *Alnus*. The constancy of the *Fagus* curve is visible in figure 2, in which *Alnus* has been removed from the tree pollen sum.

On the other hand, an increase in *Alnus* flattens actually existing maxima of trees on the slopes. If we take *Alnus* in the tree pollen sum it is possible to draw a wrong conclusion about the history of the forests.

The necessity of removing *Alnus* does not exist if the *Alnus* curve is a constant one. The curves of the other trees are not influenced in that case. As the absolute value of percentages is of no importance, removal of *Alnus* is necessary even when the *Alnus* curve is a very high one. A disadvantage of removing *Alnus* is the necessity of counting more pollen for each spectrum, especially when *Alnus* occurs in high percentages. If the peat is containing little pollen, the remaining pollen sum becomes too small to calculate meaningfull percentages. The same explanation given for *Alnus* holds for *Salix*. As *Salix* in the diagram shows no variations it has not been removed.

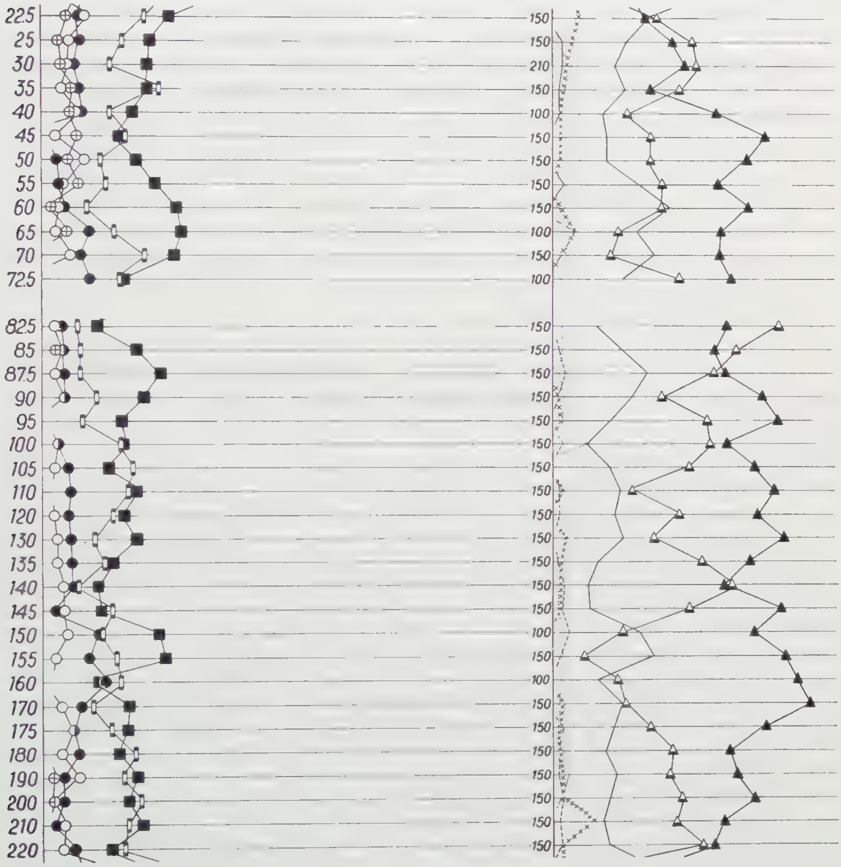

Fig. 2. Pollen diagram of Nuth, excluding *Alnus* from the tree pollen sum.

The method of removing *Alnus* should not be a general rule. It seems to me that it may be done only in regions where it is clear that the trees growing in the bog are of a different species from those outside. It is possible that, when applied to large bogs the method will give erroneous results, because either such bogs are treeless or *Alnus* grows outside the bog as well. In a recent publication Fries (1958) removed *Alnus* and *Salix* too in consideration of the supposed local overrepresentation of two genera. I do not know whether in Väster Götland *Alnus* and *Salix* are restricted to small areas like in South Limburg. In any case in some of his diagrams the curves show the same dependence on the curve of Alnus. Anyhow, in a hilly landscape like South Limburg the removal of *Alnus* is nearly a necessity.

Finally it has to be said that comparison with other diagrams in which *Alnus* has not been removed may become difficult. Concerning the trees taken into the tree-pollen sum, the reverse happened in the past with *Corylus*, however with other considerations (Faegri and Iversen, 1950; Jonker, 1952). Indeed the comparison of diagrams with tree-pollen sums containing different tree pollen is difficult. When we want to compose a diagram in a different manner from the usual, we must give a "normal" diagram as well.

The herbs and the remaining parts of the diagram will be discussed in a later paper.

REFERENCES

Faegri, K. and J. Iversen. 1950. Text-book of modern Pollen Analysis, Copenhagen: 68.
Fries, M. 1958. Acta Phytogeog. Suecica **39**.
Jonker, F. P. 1952. Taxon **1** (6): 89.

JONKER, F. P.: The genus Rhizophora in Suriname

The peculiar distribution of the species of *Rhizophora* (*Rhizophoraceae*) is well-known. Floras and manuals usually mention one western species — *R. mangle* L. — that occurs both in the coastal regions of tropical and subtropical America and in the corresponding habitats of west tropical Africa, and an eastern species — *R. mucronata* Lam. — occurring both in tropical Asia and in east tropical Africa. It is also well-known that a few other species occur in tropical Asia; a recent revision has been given by Hou (1958). G. F. W. Meyer (1818) described from British Guiana a second American species, *R. racemosa*, differing in the inflorescence which is forked and 2-flowered in *R. mangle* and much-branched in *R. racemosa*. Engler (1876) regarded this species as a variety of *R. mangle;* most botanists, however, considered it synonymous with the latter. Leechman (1918) published an investigation of the Rhizophoras of Georgetown, British Guiana. He found not only the two species of Meyer but also a third species, *R. harrisonii* Leechm., provided with a much-branched inflorescence as in *R. racemosa*. The hypocotyls (also considered radicles) of both *R. mangle* and *R. harrisonii* reach a length of up to 30 cm, that of *R. racemosa* a length of up to 65 cm. The opinion of most botanists, however, remained unchanged: namely that the material of the genus *Rhizophora* from both America and West-Africa belongs to one species, *R. mangle* L. In treating the *Rhizophoraceae* for the Flora of Suriname I shared this opinion (Jonker, 1942).

In 1953, however, Keay published his revision of the West-African Rhizophoras based on field observations. He concluded that the three species recognized by Leechman also occurred in West-Africa. Savory (1953) studied the ecology of *Rhizophora* in Nigeria and found that the most common species is *R. racemosa*, a pioneer at the outer border of the *Rhizophora* zone. *R. harrisonii* is dominant in the middle region and *R. mangle* in the interior part of the zone. The latter has the highest salt tolerance and occurs in the habitats with the highest salt concentration in the dry season. The other species obtain, especially in the wet season, more fresh water.

These two recent publications gave me a reason to revise again the Suriname material and at my request Mr. L. W. M. Bouwman studied the herbarium material and arrived at the conclusion that he could recognize the three entities. He was uncertain, however, whether they should be accorded specific rank.

During a short visit to Suriname, from November 1955 to March 1956, I was in a position to study the problem in the field. On January 31st, 1956, I visited the mouth of the Suriname River, N. of Paramaribo, in the former plantation Purmerend. *Rhizophora* occurred along the river bank as well as in the *Avicennia* forest. Especially the trees along the bank were fruiting abundantly. The inflorescence was usually 2-flowered, occasionally 3- or 4-flowered but then the 3 or 4 pedicels were inserted together. The material apparently belonged to one species. On February 10th I visited the banks of the Commewijne River between Marienburg and Kroonenburg. Here the three species occurred together and proved to be easily recognizable. The most common one was *R. harrisonii* Leechm. characterized by its large, loose, spreading inflorescences provided with slender branches and pedicels, the acute flower buds and the yellowish-green midribs. The second in number, *R. racemosa* G. F. W. Mey., is characterized by the short and thick inflorescence branches and pedicels and, consequently, contracted inflorescences provided with smaller, obtuse flower buds. The trees gave a darker impression chiefly caused by the red midribs and petioles of the younger leaves, and the red leaf buds. In older leaves the midribs and petioles are yellowish-green. Contrary to Keay's observations I never saw distinctly red midribs in *R. harrisonii.* The less common was *R. mangle* L., a species with a forked, 2-flowered inflorescence which was found to be rarely 1-, 3- or 4-flowered. On March 4th I investigated the upper part of the Commewijne River between Kroonenburg and the Matapica River and also the banks of the latter and of the Matapica canal. The situation along that part of the Commewijne River is as along the lower part. Along the Matapica River *R. harrisonu* is common. In the dense vegetation of this species one observes a few scattered trees of *R. mangle,* at once recognizable by the many fruits with brown hypocotyls, and comparatively few *R. racemosa.* Along the Matapica canal which leads to the ocean, an *Avicennia* forest occurs with a few scattered trees of *R. mangle.* On February 16th I investigated the lower Nickerie River between Wageningen and Nieuw Nickerie. Near Wageningen only a few withering *Rhizophora* trees occur, downstream the number increases and between Paradise and Nieuw Nickerie the banks are covered with a dense Rhizophora vegetation, consisting of *R. racemosa* only. This species is characterized not only by its red midribs, petioles and flower buds, its contracted inflorescences and its obtuse flower buds but also by the often very long hypocotyls.

On February 2nd I studied the banks of the lower Saramacca River between Carl Francois and Calcutta (left bank) — Huwelijkszorg (right bank). The richest *Rhizophora* vegetation was found on the right bank, situated before an *Avicennia* forest with, sometimes, some *Laguncularia* bush at the river side before the *Rhizophora. R. racemosa* and *R. harrisonii* were mixed together without a marked difference in the habitat. The river between Carl Francois and the mouth showed, below Carl Francois, at first the same situation as upstream but still more downstream *Rhizophora* disappeared. Near the mouth, however, *Rhizophora* made its appearance again but now only *R. mangle* occurred. Therefore I presumed that the same situation occurred along the Suriname River from where I knew already the *R. mangle*-vegetation near the mouth. A boat trip on this river, from Jodensavanne downstream confirmed this presumption. *Rhizophora* made its appearance near Carolina where the first scattered treelets of *R. racemosa* were observed. More downstream the vegetation becomes denser. From the boat I only observed *R. racemosa*, as along the Nickerie River, but *R. harrisonii* also occurs as appears from a collection from La Liberté by J. and P. A. Florschütz. N. of Paramaribo these two species are replaced by *R. mangle*. The latter is, consequently, found in the more saline regions as in tropical Africa, but these regions are situated in Suriname near the coast along the river mouths. *R. harrisonii* and *R. racemosa* are found in the less saline zone upstream to circ. 60 km from the coast. Along the Wayombo River also a *Rhizophora* vegetation occurs.

In those areas of a river, where *Rhizophora* occurs on one bank only, one may often observe that in the river bends the *Rhizophora* vegetation crosses the river according to the currents which bring more saline water.

A short visit to the isle of Curaçao showed that there only *R. mangle* occurs, around the bays. From a study of herbarium material it appeared that also in the other smaller West-Indian Islands and in Florida only this species occurs. The two other species, being less salt-tolerant are found in America somewhat downstream along the larger rivers. Added to these ecological preferences are the following morphological differences:

R. mangle: inflorescences forked, 2-flowered, occasionally 1-, 3- or 4-flowered. Flowers large; calyx yellow; corolla white. Midrib and petiole yellowish-green. Fruiting abundantly. Hypocotyl at first green, later brown, up to 30 cm long.

R. harrisonii: inflorescence much-branched, loose, many-flowered. Flower buds acute. Flowers smaller; calyx greenish-white; corolla white. Midrib and petiole yellowish-green (in the youngest leaves midribs sometimes pinkish). Fruiting rather rarely. Fruit smooth. Hypocotyl green, up to 35 cm long.

R. racemosa: inflorescence much-branched, contracted, many-flowered. Flower buds small, obtuse. Flowers rather small; calyx greenish-white; corolla white. Leaves darker green above than in the preceding species; midribs, petioles and leaf buds red. Fruiting rather rarely. Fruit rough. Hypocotyl green, up to 50(65) cm long.

For illustrations, see KEAY (1953).

REFERENCES

ENGLER, A. 1876. *Rhizophoraceae* in Martius, Flora Brasiliensis **12.2**: 426.
HOU, Ding. 1958. Flora Malesiana, ser. 1, vol. **5**^{4}: 429.
JONKER, F. P. 1942. *Rhizophoraceae* in Pulle, Flora of Suriname **3.2**: 36.
KEAY, R. W. J. 1953. Kew Bulletin: 121.
LEECHMAN, A. 1918. Kew Bulletin: 4.
MEYER, G. F. W. 1818. Primitiae Florae Essequeboensis, Göttingen: 185.
SAVORY, H. J. 1953. Kew Bulletin: 127.

BOOK REVIEWS

OF PUBLICATIONS RELATED TO BOTANICAL WORK IN THE NETHERLANDS

Backer, C. A.: Dutch-English taxonomic-botanical vocabulary. 2nd ed. Bogor, 1956 (1958). Bound, mimeogr., 8°, pp. 1–275. Dfl. 10.–, to be ordered with the Flora Malesiana Foundation, Rijksherbarium, Nonnensteeg 1, Leyden, Holland.

A glossary of Dutch terms with their English equivalents in the fields of taxonomy, ecology, and plant geography, mainly used in descriptions of plants. It contains over 4.000 entries. The first edition appeared in 1949 and was issued by the Rijksherbarium & Flora Malesiana in 125 copies. The second, much enlarged edition has been printed by Bibliotheca Bogoriensis, Bogor, in 300 copies, and is intended mainly for educational purposes. v. St.

Lanjouw, J. (ed.): Flora of Suriname (Netherlands Guyana), founded by A. A. Pulle, vol. 1, pt. 2, p. 93–292, 1957. Published for the van Eedenfonds by the Royal Tropical Institute, Amsterdam, Meded. No. 30 Afd. Tropische Producten No. 11. Dfl. 16.–. To be ordered from E. J. Brill's Publishing Co., Leiden.

Contents: *Batidaceae* (final page, F. P. Jonker), *Bromeliaceae* (L. B. Smith, p. 94–148), *Marantaceae* (A. M. E. Jonker–Verhoef and F. P. Jonker, p. 149–208), *Phytolaccaceae* (A. L. Stoffers, p. 209–217), *Piperaceae* (T. G. Yuncker, p. 218–290), *Chenopodiaceae* (J. Lanjouw, p. 291–292). As usual keys to the genera and species are given, with detailed descriptions of all species collected or recorded from Suriname, together with their literature, synonymy, distribution and an enumeration of all collections.

The new taxa: 3 new species and 1 new variety in *Bromeliaceae*, a new genus with 3 new specific combinations in *Marantaceae* and 1 new species in *Piperaceae* have been described recently in Acta Botanica Neerlandica and in Mededelingen van het Botanisch Museum en Herbarium Utrecht. A number of endemic *Piperaceae* were described already by T. G. Yuncker in his former publications dealing with this family. F. P. J.

Steenis, C. G. G. J. van (ed.): Flora Malesiana ser. I, vol. 5, part. 5. 8°, pp. (jl)–(11), ccxxxv–cccxlii, 381–595. 1957–1958. Dfl. 37.50; binder Dfl. 6.–. N.V. de Erven Noordhoff, Publishers, Groningen, Holland.

This is the final, voluminous instalment of volume 5, including the title-page, dedication, abbreviations & signs, supplement to the cyclopaedia of Malaysian collections and collectors, taxonomic revisions, addenda & emendanda, and general index. As usually it is profusely illustrated. The volume is dedicated to the memory of Prof. A. A. Pulle, who is mainly responsible for the revival of botanical interest in Holland for tropical floras and who raised the school of senior present Dutch taxonomists. Among the revised families the *Rhizophoraceae*, *Connaraceae*, and *Hydrocharitaceae* are the largest. Great pains have been taken to elucidate ecological problems in the *Rhizophoraceae* and *Hydrocharitaceae*. The smaller plant families comprise *Batidaceae*, *Restionaceae*, *Centrolepidaceae*, and *Erythroxylaceae*. A considerable number of plant names have been reduced and a few new species or new combinations proved necessary. There are various new records for Malaysia of species, genera, and even of a family.

For those persons who only possess volume I of the Flora Malesiana, reprints have been made with separate cover of the Supplement to it (108 pp.), which can be obtained at Dfl. 10.- with the Flora Malesiana Foundation, Rijksherbarium, Nonnensteeg 1, Leyden Holland. v. St.

Steenis, C. G. G. J. van: Vegetation map of Malaysia 1/5.000.000. In colours. Size 69½ by 124 cm. Printed in Holland with the aid of Unesco for the Unesco Humid Tropics Project. 1958. With Commentary, 8°, pp. 8. Sold by Unesco.

The map intends to give primarily a reflection of physiognomy of the vegetation actually present, based on its structure. In the main type, the rain-forest, 8 subtypes have been indicated by signatures or hatching viz. dominance by *Dipterocarpaceae*, *Agathis*, *Eusideroxylon*, *Casuarina junghuhniana*, *Pinus merkusii*, *Metroxylon*, and freshwater swamp-forest. By other colours have been indicated mangrove forest, secondary forest, savannahs, grassland, alpine grassland, monsoon-forest, teak-forest, wet rice-fields, dry fields and plantations. In all 18 types. In the commentary the status and characteristics of each of these types has concisely been discussed. v. St.

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EFFECT OF VERNALIZATION AND DAYLENGTH ON NUMBER AND SHAPE OF LEAVES IN CHICORY AND ENDIVE

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(*Publication 189, Laboratorium voor Tuinbouwplantenteelt,*
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(*received January 22nd, 1959*)

INTRODUCTION

Some years ago HARTMAN (1956) found that vernalization has pronounced after-effects on leaf morphology in chicory, *Cichorium intybus* L. In 1956 a small experiment to test these observations not only confirmed Hartman's results but led to the additional observation that vernalized plants formed a smaller number of leaves per unit of time than unvernalized ones. As a consequence there was a steadily increasing difference in size between plants belonging to the two groups.

As it seemed worth while to confirm and extend this incidental observation, an experiment was undertaken in 1957 with both chicory and the related species endive, *Cichorium endivia* L. This was followed in 1958 by an experiment designed to give more data on the effect of daylength on leaf number in these two species.

MATERIAL AND METHODS

The varieties used were chicory "Selectiva" and endive "Fullheart No 5", both from the firm of Nunhem, Haelen (L.), Netherlands. Seed was soaked during 6 hours and presprouted at 26° C during 24 hours. In 1957 the germinating seed was vernalized at 1° C during 0, 2 or 4 weeks. In 1958 endive seed was subjected to 5° C during 0, 2 or 6 weeks and chicory seed was vernalized during 0, 2, 4 or 8 weeks. The treatments were so timed that all groups of one experiment could be sown on the same date. In 1957 all seed was sown on May 22; in 1958, endive seed was sown on June 23 and chicory seed on July 7.

Plants were grown in pots placed on lorries that were in the open from 8 AM to 4 PM and were then rolled into sheds where plants receiving a long-day treatment were subjected to 8 hours of weak light from incandescent lamps followed by 8 hours of darkness, while groups receiving a short-day treatment were in darkness during the whole 16-hour period. In 1957 there were 25 plants per treatment; in 1958 10 plants out of each group were studied.

RESULTS

1. Chicory

In 1957 the number of fully grown leaves was counted every two weeks. To preclude mistakes caused by dying off of the oldest leaves, after each counting a hole was punched in the youngest leaf counted. The results are given in Table I.

TABLE I

Increase in leaf number of chicory after various vernalization treatments (daylength: 8 hours)

Days after sowing / Pretreatment at 1° C	30	54	68	82	96
0 weeks	4.8	10.4	15.8	20.2	24.0
2 weeks	4.3	9.6	15.2	20.3	24.3
4 weeks	4.4	9.3	14.4	18.2	21.9

It is clear that plants vernalized during 4 weeks form a smaller number of leaves than the other groups, but the difference is not large.

In 1958 the differences were more pronounced. Leaf numbers were counted only once, viz. 70 days after sowing. This time not the number of fully grown leaves was established, but the total number of leaves and leaf primordia longer than 3 mm. The data are given in Table II.

TABLE II

Number of chicory leaves > 3 mm 70 days after sowing following various vernalization treatments

Weeks at 5° C / Daylength	0	2	4	8
8 hours	12.5	12.9	10.6	
16 hours	27.5	24.8	15.7	15.1
natural long day	13.4	11.4	8.0 ¹)	9.7 ¹)

¹) very few plants.

There is a clear effect of vernalization in all groups, but also a striking difference in leaf number between plants in 8 hours of daylight and in 8 hours of daylight + 8 hours of incandescent light. On the other hand, plants grown in natural long day have a much smaller leaf number than those in artificial long day, but this can probably be explained by the fact that the former were subjected to lower night temperatures than those in the sheds.

2. Endive

In 1957 an experiment was designed to determine whether the after-effects of low temperature on leaf morphology, found by HARTMAN (1956) in chicory, occur in endive also. Not only was the number of leaves established, but other characteristics of the leaves were observed also. This led to the results given in Table III.

TABLE III

Effect of vernalization on vegetative characters of endive after 3 months in 8-hour days

Length of vernalization Characteristic	0 weeks	2 weeks	4 weeks
Number of leaves	52	51	34
Fresh weight per plant	55.5 g	44.5 g	32.0 g
Leaf length	10.3 cm	10.5 cm	11.9 cm
Leaf width	6.5 cm	6.9 cm	8.2 cm
Leaf thickness	185 mu	170 mu	150 mu

These data show that vernalized endive plants formed a smaller number of leaves than unvernalized plants and consequently had a lower fresh weight. Moreover leaves of vernalized plants were longer, broader and thinner than those of unvernalized plants. They were also smoother, more upright and slightly more pilose, although the effect of vernalization on the number of hairs was not nearly as pronounced as in chicory.

These observations were confirmed in 1958. Fresh weight and number of leaves > 3 mm were established only once, viz. 80 days after sowing. The data are given in Table IV.

TABLE IV

Effect of vernalization and daylength on fresh weight and number of leaves > 3 mm of endive

Length of vernalization Characteristic	0 weeks	2 weeks	6 weeks
		Daylength 8 hours	
Leaf number	72.0	64.3	44.5
Fresh weight	70.0 g	85.0 g	65.0 g
		Daylength 16 hours	
Leaf number	33.9	27.5	bolted
Fresh weight	41.8	33.3	

Except for the weight of the unvernalized group in short day, which is unexpectedly low, the differences in fresh weight reflect those in leaf number. Both vernalization and long day cause an increase in length and width of the leaves, but these differences are small in comparison to the decrease in leaf number. The difference in length between leaves of the same rank on vernalized and unvernalized rosettes is given in Fig. 1 and 2.

It follows from the data in Table III that leaves from vernalized plants are broader than those from unvernalized plants, not only in the absolute but also in the relative sense. This was also confirmed in 1958, as shown by Table V.

The ratio of length to width is smaller (i.e., the leaf is relatively broader) in long day than in short day, while in both daylengths vernalization lowers the ratio, i.e. causes broader leaves.

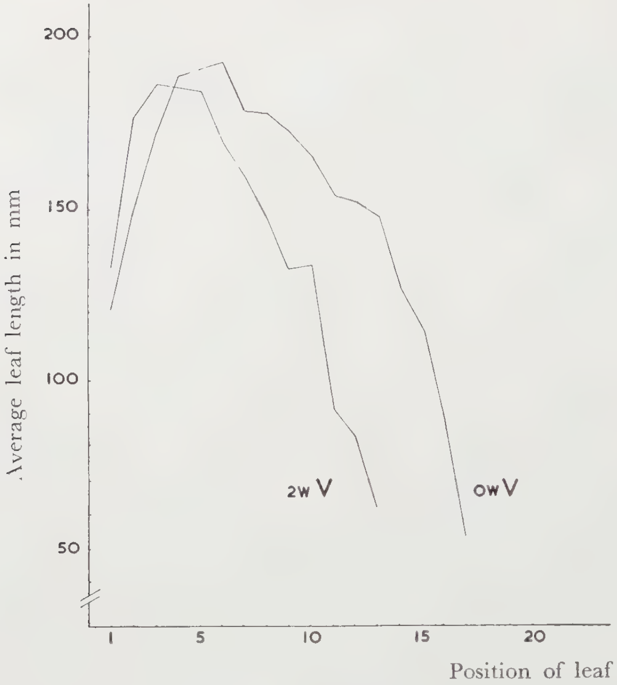

Fig. 1. Average length of mature leaves according to position on plants subjected to seed vernalization at 5° C during 0 or 2 weeks. Daylength: 16 hours (8 hrs strong light + 8 hrs weak light).

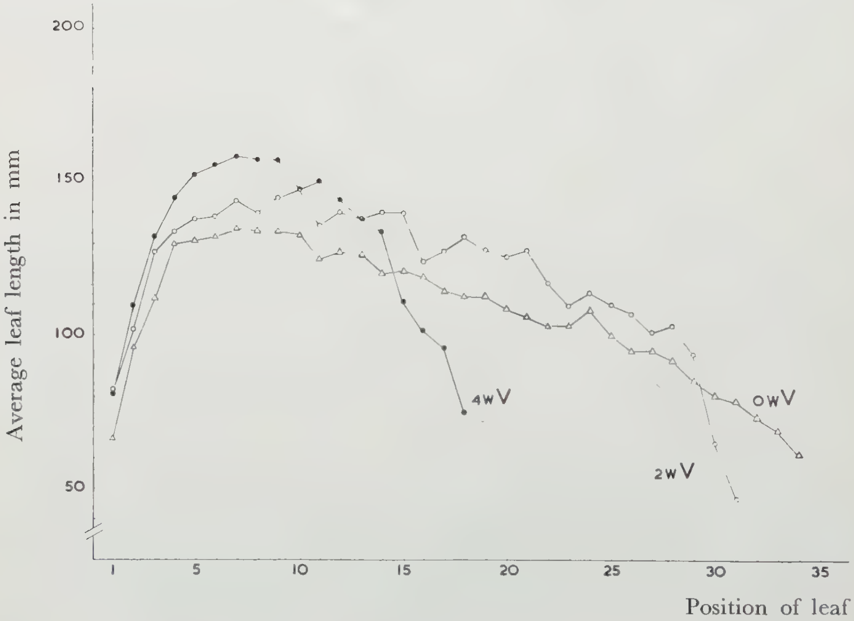

Fig. 2. Average length of mature leaves according to position on plants subjected to seed vernalization at 5° C during 0, 2 or 4 weeks. Daylength: 8 hours (strong light).

TABLE V

Length/width-ratio of endive leaves under various conditions

Position of leaves / Treatment	1–5	6–10	11–15
		Daylength 8 hours	
Unvernalized	1.95	1.80	1.77
2 weeks 5° C	1.93	1.89	1.86
6 weeks 5° C	1.77	1.73	1.76
		Daylength 16 hours	
Unvernalized	2.03	2.07	1.88
2 weeks 5° C	1.98	2.01	1.77

DISCUSSION

The interesting fact about the influence of low temperature is that it does not become apparent until later, at a higher temperature. At the moment the seed is subjected to cold there are no leaf primordia present. Apparently low temperature induces a change in the apical meristem which is irreversible, at least under the conditions of the experiments described (WELLENSIEK, DOORENBOS and ZEEVAART, 1956). How far this may be said of the influence of daylength also is not yet known. The assumption that low temperature acts directly on the meristem, but that daylength exercises its effect via the leaves, seems reasonable but has not been proven. Further research on this point and on the many other problems that arise from the results under discussion is now in progress.

SUMMARY

A study was made of the effect of seed vernalization and subsequent daylength on leaf number in vegetative plants of chicory and endive. In both species, vernalization and long day led to a marked decrease in number of leaves formed per unit of time. This corresponded with a decrease in fresh weight of the plant. The after-effects of low temperature on leaf morphology in chicory found by HARTMAN (1956) have been confirmed. In endive, vernalization leads to leaves that are longer, broader and thinner than those of unvernalized plants.

REFERENCES

HARTMAN, TH. A. 1956. After-effects of low temperature on leaf morphology of Cichorium intybus L. Proc. Kon. Ned. Akad. v. Wetensch., Amsterdam **C 59**: 677–684.

WELLENSIEK, S. J., J. DOORENBOS and J. A. D. ZEEVAART. 1956. L'action du froid dans le processus de la vernalisation. Bull. Soc. Franç. de Physiol. Végét. **2**: 1–13.

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DIFFUSIBLE AND EXCHANGEABLE RUBIDIUM IONS IN PEA ROOTS

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(*received January 28th, 1959*)

INTRODUCTION

Since the concept of apparent free space or outer space plays every day a greater part in the research on ion uptake (BRIGGS and ROBERTSON, 1958), many investigators are inclined to assume that the ions present in the apparent free space are carried passively by the transpiration stream as a kind of mass transport (a.o. HYLMÖ 1953; EPSTEIN 1956; KRAMER 1957; KYLIN and HYLMÖ 1957).

Whereas apparent free space is by definition freely accessible for all substances dissolved in the outer solution, this space would also have a free communication with the xylem vessels. This would mean that there does not exist an ion barrier between medium and xylem vessels. The ions would, therefore, be able to move freely by means of diffusion across the root tissue.

There are, however, many data which present difficulties to this concept. It seems, in the first place, to increase the difficulties of explaining the bleeding phenomenon, an objection against their theory that has already been mentioned by the authors of the view cited above (EPSTEIN 1956; KRAMER 1957). It is difficult to see how ions could be accumulated in the xylem vessels if we were to accept this hypothesis, but even when it takes place in the way suggested by HYLMÖ (1953) viz. by accumulation in the vacuoles of differentiating xylem elements, which cells would release the ions in the xylem sap, it remains obscure how a higher concentration of ions in the xylem vessels could be maintained if a free passage of ions across the root tissue occurs. For, in that case we have to assume that an ion concentration, however it may be effected, would be leveled down very rapidly.

A second objection against the theory cited above has been given by means of experiments in which it was shown, that ions formerly accumulated in the cells, can be transported from cell to cell without leaching out to the medium. This has been shown to occur in Vallisneria leaf tissue (ARISZ 1954) and for the transport of ions from the root to the shoot (HELDER, 1958).

These observations would tend to make one cautious in regard to the rather simple and perhaps obvious conclusions to be made from the free space experiments. The experiments described in this paper will show how exchangeable rubidium ions present in the roots can be easily translocated to the shoots without important leaching out to the distilled water in which the root systems were placed.

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Material and methods

After germination in moist sand pea seedlings were mounted on wooden disks (sets of 18 seedlings on each disk were used) and cultivated in a glass-house on a half-strength Hoagland solution for 18–25 days. They were then used for the experiments.

During the uptake period, the root systems of intact plants or excised root systems were placed on a labelled rubidium chloride solution with constant aeration. After that, part of the sets were rinsed during 10 or 20 seconds in distilled water by moving them 2 or 6 times up and down, blotting them then with filterpaper. The amount of labelled rubidium present in the root systems treated this way is taken as being the ions in the apparent free space (FSI) + exchangeable ions (EI) + accumulated ions (AI).

Another part of the root systems was rinsed with distilled water during 30 to 240 minutes (time of rinsing mentioned for each experiment) and the rubidium ions present in the tissue after this treatment are taken as being exchangeable ions + accumulated ions. The accumulated fraction is defined as the amount of rubidium present in the root after washing the root systems in an unlabelled solution with the same concentration as used during the uptake period.

By subtracting the different amounts from each other, the values for apparent free space ions, exchangeable fraction and accumulated fraction were determined.

Experiments

1. *The amount of ions in the different fractions as dependent on the duration of uptake.*

Excised root systems were transferred to a 10 mM Rb*Cl solution and after various absorption periods taken out for analysis. Each time the series consisted of three sets. One was washed in distilled water during 20 seconds by gently moving the root system up and down 5 times and thereafter blotting them with filterpaper. Another set was rinsed in distilled water during 60 minutes and the third ones in 10 mM RbCl during the same time. Fig. 1 shows the amounts of Rb* ions present in the roots after the different treatments as dependent on the duration of the uptake period.

The accumulation of Rb* ions in the root tissue continues at a constant rate throughout the whole experiment. Apparent free space and exchange space, however, are fully equilibrated with the outer solution in time periods as short as 30–60 minutes. This is shown in Fig. 2. The amount of ions in the AFS and the amount of EI are more or less the same in this experiment.

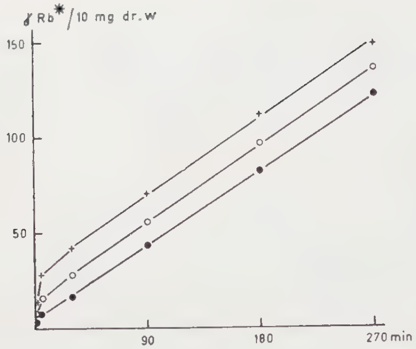

Fig. 1.

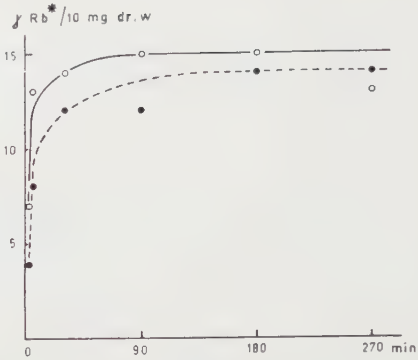

Fig. 2.

Fig. 1. Time course of the Rb* uptake by excised pea roots. Nutrient solution 10 mM Rb*Cl. Aeration throughout.

Fig. 2. Time course of the penetration of the root (Fig. 1) by FSI (circles) and EI.

2. *Further analysis of the exchangeable fraction.*

In previous experiments the amount of exchangeable rubidium was rather variable. Moreover there was a striking difference in the bleeding activity. Sometimes the root systems showed a distinct bleeding, in other cases the bleeding was very small. It was to be suspected that there would be a relation between the variability in bleeding activity and the amount of exchangeable ions in such a way, that root systems showing rapid bleeding in distilled water would contain a smaller amount of exchangeable Rb* afterwards. The root systems which were rinsed in distilled water with the cut surface below the surface of the liquid were now washed, partly with the cut surface below and partly with this surface above the solutions. Fig. 3 shows the results of such experiments. After the uptake period, part of the root systems were firmly blotted with filterpaper (FSI + EI + AI vide p. 69), another part was rinsed with distilled water during 60 minutes, i.e. group 1 with the cut surface above and group 2 with the cut surface below the water surface. The third portion was washed during 60 minutes with the unlabelled solution in the same manner, i.e. with the cut surface above or below the surface.

It appears (Fig. 3), that part of the ions which are measured as exchangeable ions in group 1 are measured as AFS-ions in group 2. This means that part of the exchangeable ions leaves the root through the cut surface if this surface is rinsed in water. This fraction may be present in the xylem vessels at the end of the uptake period and/or it represents the results of the bleeding of the root system.

In the following experiment the bleeding sap was captured and analysed separately, whereas the rootstump above the rinsing solution (about 1. cm) was analysed separately from the rest of the root tissue. The results of two experiments of this kind were plotted in Fig. 4. The differences arising from rinsing with and without uranylnitrate 10^{-3} M during a rinsing period of 45 minutes were compared.

It is clear that without inhibitor more Rb* is transported to the rootstump and more is excreted in the bleeding sap than in the presence of the inhibitor. Comparing these two treatments it is clear that the transported labelled rubidium ions are totally removed from the exchange spots and partly from the accumulated fraction (negative exchangeable fraction) without inhibitor.

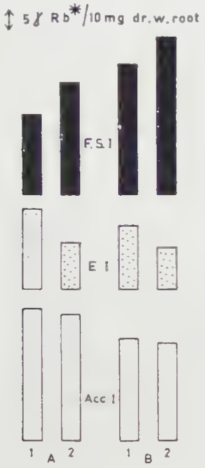

Fig. 3.

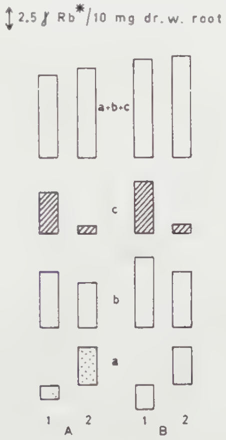

Fig. 4.

Fig. 3. Influence of the way of rinsing on the amount of Rb* ions in the different fractions viz. accumulated ions (Acc.I.), exchangeable ions (EI) and ions in the free space (FSI). 1. rinsed with the cut surface above the liquid. 2. rinsed with the cut surface immersed. A and B replicate experiments.

Fig. 4. The bleeding as a cause of the decrease in amount of exchangeable ions during a stay on distilled water. After an uptake period on 5 mM Rb*Cl during 3 hours, the roots have been rinsed 45 minutes in distilled water (1) or in 10^{-3} M uranylnitrate (2). In both cases with the cut surface above the liquid. *a.* exchangeable Rb* ions in the root tissue after the rinsing period. *b.* Rb* ions in the root stump i.e. that part of the root above the liquid surface. *c.* Rb* ions in the exudate.

Summarising the results of the experiments described in this section it is evident, that the exchangeable ions can be quantitatively transported with the bleeding stream, and that an active process takes the ions from the exchange sites into the xylem vessels (Arisz 1945, 1956, 1958).

3. *The translocation of exchangeable rubidium ions to the shoot.*

In the preceding paragraph we have seen, that the exchangeable ions can be translocated to the xylem vessels which causes an exudation at the cut surface of decapitated plants. It will be of some interest to know how this transport depends on the transpiration rate in intact plants. In the following experiment (results plotted in Fig. 5) intact pea plants absorbed Rb*Cl during 60 minutes. At the end of this period the shoots of part of these sets were excised and the roots were rinsed with distilled water or with unlabelled rubidium chloride. In this manner the amount of diffusible, exchangeable and accumulated ions at the end of this period can be known, the state of affairs being shown in Fig. 5*A*. Of the other sets the root systems were transferred to distilled water and the shoots were covered by a glass-cover (low transpiration, water uptake 2 ml/hr), or placed at free transpiration (moderate transpiration, water uptake 4 ml/hr) or ventilated (high transpiration, water uptake 7 ml/hr). This treatment lasted 60 minutes. Thereafter the exchangeable and accumulated

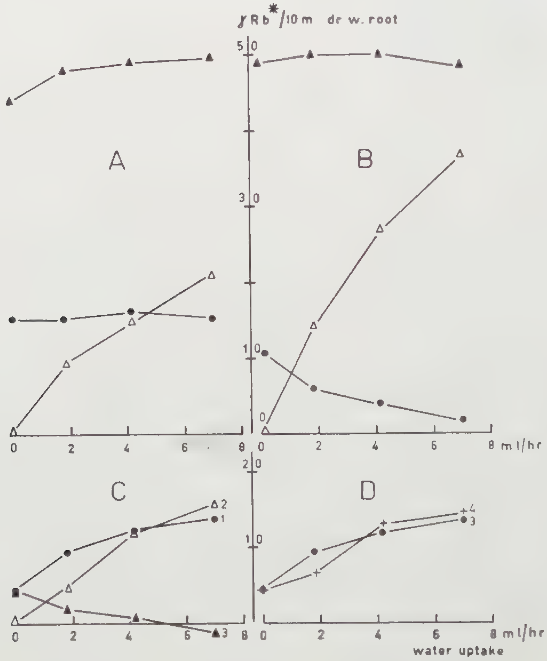

Fig. 5. Uptake and subsequent redistribution of Rb* ions in pea plants.
A. The amount of Rb* ions in the shoots (△ — △) and in the roots, the latter separated in exchangeable ions (● — ●) and accumulated ions (▲ — ▲) as measured directly after an uptake period of 1 hour on 10 mM Rb*Cl at various transpiration rates (0 ml/hr = excised root systems, 1.84 ml/hr glasscovered intact plants, 4.16 ml/hr freely transpiring plants and 7.00 ml/hr).
B. The distribution of the Rb* ions over the three fractions of Fig. 5*A* after a 1 hour uptake period on 10 mM Rb*Cl followed by a subsequent stay of 1 hour on distilled water. Transpiration treatment of the plants during both periods as indicated on Fig. 5*A*.
C. Changes in the amount of Rb* ions in the three fraction (differences between Fig. 5*A* and Fig. 5*B*) during the stay on distilled water as related to the transpiration rate. (1) decrease in the amount of exchangeable Rb* ions in the roots. (2) increase in the amount of Rb* ions in the shoot. (3) increase or decrease of the amount of accumulated Rb* ions in the roots.
D. Showing the accordance between the decrease of the exchangeable fraction (3) and the increase in accumulated + transported fraction (4).

fraction was determined in the same way as described above. The state of affairs at the end of the redistribution period is plotted in Fig. 5*B*.

It became apparent that the treatment following the uptake period resulted in a decrease of the amount of exchangeable labelled rubidium ions in the roots and that this decrease was greater with high transpiration rates than with low transpiration, the moderate transpiration lot giving values in between. In the case of the decapitated root systems on distilled water, the decrease of the exchangeable fraction corresponded with an equivalent increase of the accumulated ions. In the intact plants a competition occurs between accumulation in the root and transport to the shoot. The latter was the more pronounced the greater the transpiration rate, with the strongest transpiration the whole amount of exchangeable Rb* ions was transported in one hour to the shoot and perhaps also a little of the accumulated fraction. This transport is shown in Fig. 5*C* (difference between Fig. 5*A* and Fig. 5*B*).

By these results one seems justified to state that the exchangeable rubidium ions can be transported via the xylem vessels to the shoots without diffusing to the medium, because the loss of ions from the exchangeable fraction can be measured quantitatively as an increase in the shoots (Fig. 5*D*).

4. *The translocation of labelled rubidium ions from the roots to the shoots if both diffusible and exchangeable ions are present.*

The uptake period in this experiment again lasted 60 minutes. After that the root systems of the intact plants were gently blotted with filterpaper (the plants remained in their position on the wooden holders). Three sets were used for the direct estimation of FSI, EI and AI in the way described above. The other sets were placed in the dark with their root systems in humid air, loss of ions to the medium being impossible. After resp. 1, 2 and 4 hours three sets each time were removed for analysis of the three fractions at that moment. At the same time a series of plants remained on the radioactive rubidium chloride solution in order to be able to compare the translocation rates of the series. The results shown in Fig. 6*A* indicate that in this experiment the AFS is considerably greater than in the experiments described above. This was caused by the less effective blotting. The amount of ions in the AFS decreases continuously throughout the experiment and rectilinearly with the time. Besides it is evident that the amount of exchangeable ions did not alter. This means that in this case the transport to the shoot takes place at the cost of the ions in the AFS and not of the exchangeable ions. It remains possible, however, that the exchangeable ions are transported but are replaced from the AFS. On the basis of these experiments it is not possible however to make a choice between these two possibilities.

Comparing the results of the two series, it is evident that the rate of accumulation in the roots is somewhat greater for the plants remaining in the nutrient solution than for those with the roots in humid air. Both rates are smaller than the absorption rates during the first hour, with the shoots in the light.

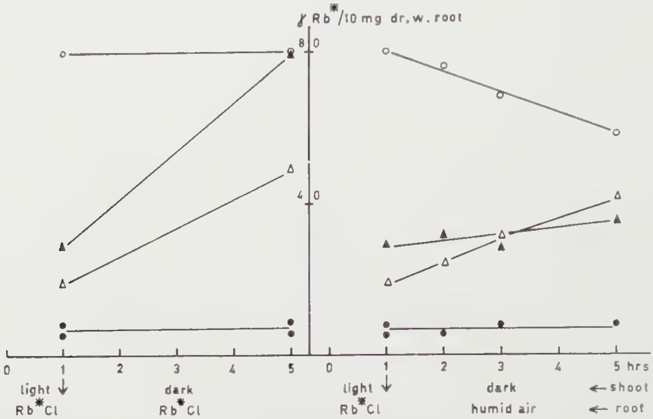

Fig. 6*A*. Amount and distribution of Rb* ions in shoots (△ — △) and roots, the latter separated in accumulated ions (▲ — ▲), exchangeable ions (● — ●), and ions in the free space (○ — ○) after a 1 hour uptake period in the light on a 10 mM Rb*Cl solution and after a subsequent 4 hour period in the dark on the same solution.

Fig. 6*B*. Amount and distribution of the Rb* ions in shoots and roots after an initial uptake period of 1 hour in the light on a 10 mM Rb*Cl solution followed by blotting of the root systems and a subsequent redistribution period in the dark with the root systems in moist air. Signals as in Fig. 6*A*. The ions present in the free space are moving to the shoots and for a part also to the accumulated fraction of the roots. The amount of exchangeable ions remains the same throughout.

Discussion

The data obtained in these experiments are in part in agreement with the results obtained by other authors. After transferring the root systems to a salt solution from a solution lacking these ions the AFS is filled up with ions in a very short time by means of diffusion. This AFS can represent a considerable percentage of the tissue, viz. 20–35 % of the root tissue of barley and wheat (Butler, 1953; Epstein, 1956; Kylin and Hylmö 1957) and a somewhat lesser percentage of bean plants (Hope and Stevens 1952) and pea plants (Hylmö 1953). The percentage found in the present author's experiments with pea plants treated in the way described above were about 7–10 % of the root volume. In accordance with the results of Epstein (1955) the ions present in the free space can be transported to the shoot or accumulated in the root cells.

In addition to the apparent free space another ion fraction is attained at the same time and with the same rate. This fraction may relate to ions adsorbed on conversely charged sites as generally suspected. It is common knowledge that the exchangeable ions can only diffuse from the tissue to the medium if they are replaced at the same time by ions of the same kind or by very similar ions. By such a behaviour this ion fraction is defined and this is used to measure this component.

Most interesting in these experiments the present author considers the fact that during a stay on distilled water following an uptake period the exchangeable rubidium ions are released from the root tissue. These ions are, however, not given off to the outer solution but are quantitatively involved in a one-way transport to the exudation sap or to the shoot. This means that these ions once in the protoplasm go much easier towards the xylem vessels than back towards the medium.

If both diffusable and exchangeable ions are present, the amount of the latter is nearly constant. This means that the diffusible ions either go straight to the xylem vessels or they replace the exchangeable ions if these are directly transported to the xylem vessels. At the moment no preference can be given to one of these two possibilities.

These experiments also give some suggestions on the localisation of the ion fractions concerned. The observation that the amount of ions in the AFS seems to be greater when the root systems are rinsed while submersed in water than when rinsed with the cut surface above the liquid and that the exchangeable fraction in the latter case is greater, is a strong indication that exudation is continued while the root system is being rinsed. It has not been proved, that the ions in the xylem vessels can be exchanged but when exudation continues new ions will be taken from the central plasm into the xylem vessels. There must be an active mechanism which transfers the ions from the surface to the vessels. Where this system is localised is still unknown. Since in addition the value of the apparent free space is so much dependent on the method of determination and seems always the greater the thinner the roots (compare barley and wheat with bean and pea) it may be suggested that the AFS is localised at the root surface and in the cell walls of the root cortex. The exchange ions might be found in the protoplasm of the root cells.

If this assumption is right, it would mean that the plasmalemma would constitute an ion barrier between medium and xylem vessels. This barrier would in that case be easily crossed by the ions going inwards much more difficult in the outward direction (WALKER 1957). This concept may aid in explaining a number of observations which seem so diversifying on first sight. The influence of the transpiration rate on the ion transport may be pronounced, as long as the entrance of ions into the protoplasm is not the limiting factor in the chain of processes involved in the ion uptake.

ACKNOWLEDGEMENTS

This investigation was carried out in 1956 and 1957 at the Botanical Laboratory, Groningen, aided by a grant from the organisation for "*T(oegepast) N(atuurwetenschappelijk) O(nderzoek)*". I wish to express my gratitude to Prof. Dr. W. H. Arisz for valuable advice and to Ir. E. W. Schierbeek (M.Sc.) for corrections to the English text.

SUMMARY

Experiments are described in which it is shown that exchangeable rubidium ions in pea roots are transported to the shoot. The rate of this translocation is dependent on the transpiration rate. The exchangeable ions are released by the tissue to the xylem vessels without leaching out towards the medium. It is suggested that this indicates the presence of an ion barrier in the plasmalemma.

The apparent free space is thought to be localised at the root surface and in the cell walls of the cortex, whereas the exchangeable ions are found in the protoplasm.

REFERENCES

Arisz, W. H. 1945. Proc. Kon. Ned. Ak. Wet. **48**: 420–446.
————, 1954. Acta Physiol. Pharmacol. Neerl. **3**: 575–599.
————, 1956. Protoplasma **46**: 5–62.
————, 1958. Acta Bot. Neerl. **7**: 1–32.
Briggs, G. E. and R. N. Robertson. 1957. Ann. Rev. Pl. Phys. **8**: 11–30.
Butler, G. W. 1954. Phys. Plant. **6**: 617–635.
Epstein, E. 1955. Pl. Phys. **30**: 529–535.
————, 1956. Passive passage and active transport of ions in plant roots. Radioactive Isotopes in Agriculture U.S. Government Printing Office, Washington.
Helder, R. J. 1958. Acta Bot. Neerl. **7**: 235–249.
Hope, A. B. and P. G. Stevens. 1952. Austr. J. Sci. Res. **B5**: 335–343.
Hylmö, B. 1953. Phys. Plant. **6**: 333–405.
Kramer, P. J. 1957. Science **125**: 633–635.
Kylin, A. and B. Hylmö. 1957. Phys. Plant. **10**: 467–484.
Walker, N. A. 1957. Nature **180**: 94–95.

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ALPINE SPECIES OF TARAXACUM

WITH SPECIAL REFERENCE TO THE CENTRAL AND EASTERN ALPS

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(*'s-Gravenhage*)

(*received December 30th, 1958*)

INTRODUCTION

In this study I do not intend to give a more or less complete survey of the *Taraxacum* species, growing in the alpine regions of Europe. Many taxa are not yet well recognized and, partly, they are insufficiently collected for description; in several cases their achenes are not available, often due to the fact that these ripen too late in the season: mostley they are flowering in July or August.

The sections, represented in these alpine regions, are listed below; only a few will be treated here in more detail. Besides material of my own, rather extensive alpine collection, I have used material of the following herbaria, in most cases only for a part; the abbreviations refer to those used in Index Herbariorum I, ed. 3, 1956 by Lanjouw and Stafleu: Instituto Botánico de Barcelona (BC); Jardin Botanique de l'Etat, Bruxelles (BR); Bündner Naturhistorisches und National-park–Museum, Chur (CHUR); Instituto Botánico Dr. Júlio Henriques, Coimbra (COI); Conservatoire et Jardin Botaniques, Genève (G); Institut für systematische Botanik, Graz (GZU); Institut Botanique de la Faculté des Sciences, Grenoble (GR); The Herbarium, Kew (K); Musée botanique cantonal, Lausanne (LAU); Rijksherbarium, Leiden (L); Botanisk Museum, Oslo (O); Muséum National d'Histoire Naturelle, Paris (P); Geobotanisches Forschungsinstitut Rübel (RUEB); Naturhistoriska Riksmuseet, Stockholm (S); Botanisch Museum en Herbarium der Rijksuniversiteit, Utrecht (U); Naturhistorisches Museum, Wien (W); Laboratorium voor Plantensystematiek en Plantengeographie, Wageningen (WAG); Botanischer Garten und Museum der Universität, Zürich (Z); Institut für Spezielle Botanik der Eidg. Technische Hochschule, Zürich (ZT).

Furthermore I was able to examine the private collections of P. Aellen, J. Duvigneaud, J. Lambinon, Prof. R. de Litardière †, Prof. H. Melzer, Dr. H. Schaeftlein and Prof. F. T. Widder.

I acknowledge with much gratitude the help of the directors of the above mentioned institutes and of the other gentlemen for the loan of their important material and for their help in some way or another. The photographs, reproduced by courtesy of the Rijksherbarium, Leiden, are made by Mr. C. L. Marks, whom I am grateful for this fine work.

Apart from the abbreviations, given above, a few are added here: h = herbarium; H. M. = von Handel–Mazzetti; v. S. = van Soest.

SECTIONS

1. **Parvula** von Handel-Mazzetti, 1907. Monogr. *Taraxacum*: 45; van Soest, 1954. Collectanea Botan. *4.1*: 13. The section is represented in the region, considered here, by only one species: *T. dissectum* Ledebour; for its distribution, see v.S., l.c.

2. **Pachera** van Soest 1954. Collectanea Botan. *4.1*: 14. The section consists of three species: *T. pacheri* Schultz-Bip.; for its distribution, see Hegi 1928. Flora Mittel-Europa *6.2.*: 1089; *T. litardieri* v. Soest 1957. Acta Bot. Neerl. *6*: 416, known from Corse and the Alpes Maritimes; the third one: *T. nevadense* Lb. f. is only known from the Sierra Nevada.

3. **Arctica** Dahlstedt 1921. Acta Fl. Suec.: 37 and 1928. K. Svenska Vet. Ak. Handl. *3.6*: 55, with 2 species in the region: *T. handelii* Murr and *T. reichenbachii* (Huter) Huter, both known from the eastern Alps, see Hegi l.c.: 1086 and v. Handel-Mazzetti 1935. Verh. Zool.-Bot. Ges. Wien 85: 26-49.

4. **Ceratophora** Dahlstedt l.c.: 34, common in the boreal and arctic regions and known from few localities in the central and eastern Alps; a new species is described below.

5. **Alpina** Haglund 1950. Ber. Schweiz. Bot. Ges. *60*: 237; species of this section are treated below in detail.

6. **Fontana** v. Soest is described as a new section; a number of species is treated here in detail.

7. **Cucullata** v. Soest is described as a new section and treated in detail.

8. **Rhodocarpa** v. Soest 1954. Collectanea Botan. *4.1*: 15 is represented by *T. schroeterianum* v. Handel-Mazzetti, a species more abundant than was mentioned earlier by H.M. l.c.: 104-105 and Hegi l.c.: 1094-1095; additional localities are given below. Under the same heading *T. rufocarpum* is described, though possibly not belonging to this section.

9. **Vulgaria** Dahlstedt (apud Lindm. 1918); Dahlstedt 1921. Acta Fl. Suec. Many species of the European plains are introduced in the alpine region; a few, seeming to be native in the subalpine and alpine districts, are treated below.

10. **Eu-Erythrocarpa** Dahlstedt 1921, Acta Hort. Bergiani *9.1*: 23. Only *T. aquilonare* v. Handel-Mazzetti is known from here; for its distribution, see Hegi l.c.: 1095; other species occur in the extreme West and East of southern Europe and in the Orient.

11. **Erythrosperma** Dahlstedt em. Lindberg f. 1935, Acta Bot. Fennica: 17; species of this section are only scarcely introduced into the higher alpine region; amongst these *T. plumbeum* Dahlstedt seems to be the most common one there.

SECTIO CERATOPHORA DAHLSTEDT

Taraxacum krättlii van Soest **nov. spec.,** Fig. 1.

Planta humilis 5–8 cm alta.

Folia ad 7 cm longa (petiolis alatis roseo-violaceis inclusa) laete gramineo-viridia, in nervo dorsali parce araneosa vel glabra. Folia exteriora oblanceolata denticulata vel breve dentata; interiora breve lobata; lobi laterales utrinque ad 4, triangulares ad 4 mm longi dorso denticulati vel breve dentati, interlobiis subnullis latis; lobus terminalis indeterminatus subobtusus paulo denticulatus interdum incisus.

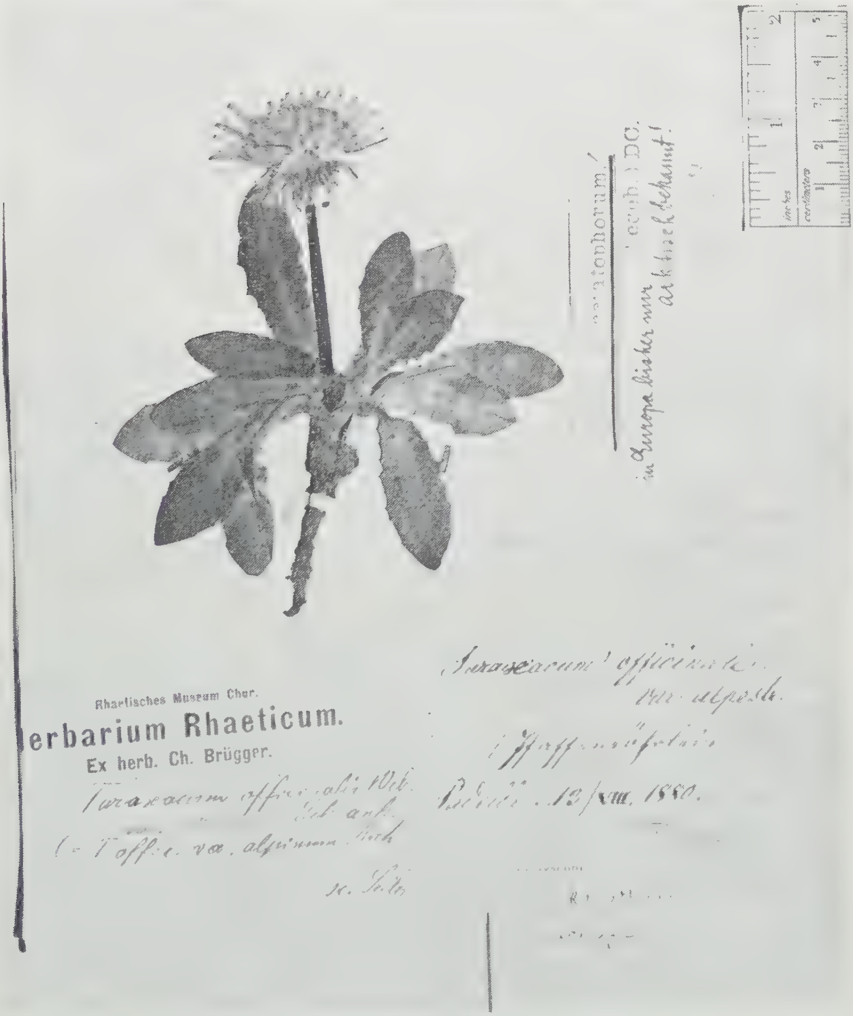

Fig. 1. T. krättlii v.S., type specimen.

Scapi ad 3 subcrassi glabrescentes.

Involucrum crassiusculum ca. 13 mm longum, 12 mm latum, obscure viride siccis nigrum. Squamae exteriores ± adpressae ovatae ad 7 mm longae, apice pro parte cornutae pro parte corniculatae vel callosae, albo-marginatae; squamae interiores late lineares, membranaceo-marginatae corniculatae vel callosae, apice obtusae saepe erosae.

Calathium paulo radians ad 3 cm diametro pallide luteum. Ligulae marginales planae extus stria pallide cano-purpurea notatae, apice obscure purpureae. Antherae polliniferae; stylus parte superiore et stigmata fusco-virescentia. Floret augusto.

Achenium (specimen 1906, Candrian!) pallide brunneum, ca. 4,5 mm longum (pyramide inclusa) superne argute et patente spinulosum ceterum rugosum—basi laeve, in pyramiden ca. 0,8 mm longam sensim abiens; rostrum ca. 7 mm longum; pappus albus 6 mm longus.

E sectione Ceratophororum Dahlstedt.

Typus: Rhaetische Alp.: Piz Padella, 13.8. 1880 Krättli (CHUR); also h. ZT; from the same mountain: 2250–2260 m, 1906 Candrian & H. M. (ZT), see also H. M., Monographie Tar., Plate 5 and Candrian 1928, Katalog Oberengadiner Fl.: 157. Furthermore: 2300 m, 1910; 2400 m, 1913 and 1915, all Branger (RUEB, Z).

This species already was recognized by H. M. as *T. ceratophorum* (Ledebour) DC, a macrospecies standing for the whole section.

Remark. In the same region a form has been collected with few and small appendices on the involucral bracts, suggesting a transition between *T. krättli* and an other alpine species. Though *Taraxacum* in general is highly apomictic, transition forms may not be excluded. Mutations are known, for instance in normally triploid *Vulgaria*, which partly and to some degree can produce crossings, resulting in partly viable apomictic products.

Sectio Alpina Haglund

A description of *Leontodon alpinus* Hoppe has been published in Sturm 1821. Deutschlands Flora. Hoppe's herbarium has been included in that of the Botanical Institute of Graz (GZU); however the labels have been mutilated in some way or another, as Prof. Widder has kindly communicated to me; so, there is no real possibility to reconstruct Hoppe's type specimen in this collection. Happily, I know some plants, collected by Hoppe, send by him to Koch, and now in the Rijksherbarium at Leiden; a sheet contains a few specimens and a label, written by Koch: "*alpinum ab autore Hoppio*". The plants belong to three different microspecies, all belonging to sect. *Alpina*.

Afterwards, Hegetschweiler and Heer 1840. Fl. der Schweiz: 762 have introduced the name *T. alpinum*, but Becherer 1952. Ber. Schweiz. Bot. Ges. 62:581, showing that this name is not valid, has proposed: *T. palustre* (Lyons) Symons ssp. *Hegetschweileri*.

In his monography v. Handel–Mazzetti has treated *T. alpinum*

as the others authors in its broad sense, more or less aequivalent to the whole section *Alpina*, described by Haglund.

Key to the species of sect. Alpina

(as far as mentioned in this paper)

1. Pollen absent 2

Pollen present 5

2. Flowers without or with pale grey or clear purple stripes underneath 3

Flowers with dark brown- or bluish-violet stripes underneath 12

3. Flowers lingulate 4

Flowers tubular; leaves lobate, lobes triangular, acute; terminal lobe acute . . . . 5 *T. oreophilum*

Remark: few other forms with tubular flowers have been found, partly (?) being aberrations; see also sect. *Cucullata.*

4. Involucre dark, black in dried condition; flower heads radiate . . . . 14. *T. vetteri*

Involucre green, flower heads small, non radiate . . . . 4. *T. mattmarkense*

5. Flowers without or with pale grey or pink stripes underneath . . . . 7. *T. parsennense*

Remark: compare also . . . . 2. *T. carinthiacum*

Flowers with dark greyish-violet, -purple, or -blue stripes underneath 6

6. Stigmas clear yellow . . . . 9. *T. pseudofontanum*

Stigmas dirty yellow, even in dried condition 9

Stigmas (and upper part of styles) dark, in dried condition black 7

7. Leaves deeply lobate, lateral lobes narrow, terminal lobe relatively big; flowers tubular or nearly so; outer bracts of the involucre narrow, lanceolate, narrowly margined . . . . 13. *T. vernelense*

Leaves nearly entire or sublobate, flowers lingulate . . . 8

8. Outer bracts of the involucre dark green without margine, ovate, appressed; leaves not thin, grass-green . . . . 3. *T. helveticum*

Outer bracts of the involucre pale green, with pale margine, ± recurved, oblanceolate; leaves thin, yellow-green . . . . 10. *T. saasense*

9. All leaves with distinct and narrow petioles, obovate, not or only scarcely dentate, seldom sublobate . . . . 8. *T. petiolulatum*

Leaves distinctly lobate 10

10. Lobes short, lingulate, obtuse or nearly so, mostly entire; outer bracts of the involucre appressed . 12. *T. venustum*

Lobes triangular, acute, often with recurved apex 11

11. Rostrum at least 6 mm 13

Rostrum at most 6 mm 12

12. Lobes mostly slightly recurved . . . . . 6. *T. panalpinum*
    Lobes (of the leaves on the same plant) spreading outwards and partly upwards, seldom partly recurved . . . . 2. *T. carinthiacum*
13. Achenes (except cone) nearly 4,5 mm long; involucre nearly 14 mm long; bracts partly with appendices; leaves yellowish green . . . . 1. *T. apenninum*
    Achenes (except cone) nearly 3 mm long, involucre nearly 11 mm long, bracts without appendices; leaves grass-green . . . . 11. *T. vereinense*

1. **Taraxacum apenninum** (Tenore) DC. *emend.* v. Soest;

Leontodon apenninum Tenore 1830; *Taraxacum apenninum* DC. 1838; E. & A. Huet du Pavillon, Pl. Neapol. exsicc. 380, pro *T. apennino* Tenore; non *T. apenninum* Tenore 1845 and v. Handel-Mazzetti 1923 et aut.

The descriptions by Tenore and by De Candolle, are insufficient; therefore I have to give a more detailed one, which I have based on the exsiccatum of Huet du Pavillon, very similar to the plant—not very well developped—collected by Tenore and used by De Candolle for the decription in his Prodrome. The exsiccatum, furthermore, seems in full agreement with the icones in Tenore, Fl. Neapolitana 5, tab. 182, Fig. 1.

There has been a confusion with *T. glaciale* E. & A. Huet du Pavillon, exsicc. 377 by several authors, a species without rostrum, even by Tenore himself.

Planta mediocris ca. 8–12 cm alta, parce araneoso-pilosa.

Folia numerosa ad 15 cm longa (petiolo pallido angusto vel subalato vel pro parte conspicue alato inclusa), luteo-viridia, lingulata multilobata; lobi laterales utrinque ad 6, breves deltoidei vel triangulares, saepe obtusi vel subobtusi, inferiores acuti dentati vel denticulati, interdum dorso grosse dentati, margine inferiore integro, in interlobiis ad 6 mm latis abeuntibus; lobus terminalis subobtusus subhastatus vel indeterminato-deltoideus, lobuli basis breves.

Scapi floriferi foliis breviori, sub involucro saepe glabri.

Involucrum mediocre ad 14 mm longum, ad 10 mm latum, basi subtruncatulum, viride. Squamae pro parte callosae, exteriores laxe adpressae oblanceolatae vel ovatae, ad 6 mm longae, ad 4 mm latae, obtusae, albo-, roseolo- vel pallide marginatae; squamae interiores late lineares, membranaceo-marginatae.

Calathium paulo radians. Ligulae marginales angustae, planae, extus stria obscure cano-purpurea notatae. Antherae polliniferae; stigmata sordide lutea. Floret aestate.

Achenium stramineum ca. 4,5 mm longum (pyramide exclusa), superne spinulosum, in pyramiden conicam ca. 0,7 mm longam subsensim abiens. Rostrum 7 mm longum; pappus albus, 5 mm longus.

E sectione Alpinorum Haglund.

Typus: in pascuis ad noves montis Corno (25 2800 m), Apruti, 26.8.1856 Huet du Pavillon, Pl. Neapolitani no. 380 G, K, P, W, WAG); from the same place, 27.8.1856 Huet du Pavillon (G, as *T. officinale var. alpinum* Koch).

Furthermore I have seen: Apruc., 1833 Tenore (h.DC); Majella, Valle di Femina Morte, 1924 H.M.(W), in company with *T. glaciale* Huet du Pavillon: they are labelled by H.M. respectively as: *T. alpinum* and *T. apenninum*!

2. **Taraxacum carinthiacum** van Soest **nov. spec.**

Planta mediocris glabrescens.

Folia numerosa sublutescentia subglabra, petiolis pro max. parte alatis, pro parte late alatis, nervoque mediano pallido. Folia eaedem plantae valde variabilia, lobata; lobi laterales utrinque plerumque 3–4, saepe deltoidei breves vel triangulares sublongi (summo saepe sublingulato), erecto-patentes vel retroversi, integri vel margine inferiore vel superiore 1–2 dentibus muniti; interlobiis interdum indeterminatis integris vel 1–2 dentibus munitis vel sublobatis; lobus terminalis indeterminatus saepe ± depresso-rhomboideus, integer vel sublobatus, interdum lobuli basis subovati distincti.

Scapi foliis subaequilongi, glabri vel sub involucro parce araneosi.

Involucrum mediocre ad 13 mm longum ad 15 mm latum, obscure viride saepe subglaucescens. Squamae exteriores erecto-patentes interdum apice recurvatae, lanceolatae vel ovato-lanceolatae ad 6 mm longae, anguste vel angustissime albo- vel viride marginatae; squamae interiores late lineares.

Calathium planum radians ad 3,5 cm diametro obscure luteum. Ligulae marginales planae extus stria cano-purpurea notatae. Antherae parce polliniferae. Stylus parte inferiore aureus, superiore luteo-virescentia, stigmata sordide lutea vel fuscescentia. Floret aestate.

Achenium (speciminis non typici) stramineum 4 mm longum (pyramide inclusa) superne subspinulosum ceterum laeve, in pyramiden conicam ca. 0,5 mm longam subsensim abiens; rostrum 5–6 mm longum, pappus albus 5 mm longus.

E sectione Alpinorum Haglund.

Typus: Hohe Tauern: Mallnitzer Tauerntal, slopes of Geiselkopf 1900 m, 18.7.1957 v. Soest (h. 38034; also 38016-7, 38019, 38030).

Furthermore:

Alp. de Savoie: Dent d'Octre 2000–2200 m, 1904; Pas de la Bosse 1700 m, 1899; Lac de Soix 2250–2260 m, 1905, all Briquet (G); Col d'Iséran, 1884 Perrier (G); Col de la Vanois-Tarentaise, 1889 Fauconnet (G).

Berner Alp.: Paneyrossaz, Alp. de Bex, 1835 Muret, also de Charpentier; the same valley 2210 and 2290 m, 1943 Villaret; Outans 1970 m and Vallée de l'Etivaz, Seron 2060 m, both Maillefer, all (LAU).

Walliser Alp.: Betlihorn, 1891 Chenevard (G); St. Bernard, 1843 Reichenbach f. (W).

Glarner Alp.: Graue Hörner, 1857 Alioth (G).

Rhaetische Alp.: Cucal Nair, Val Avers 2500 m, 1895 v. Tavel (ZT); Albula 2300 m, 1892 Meyer (ZT); Albula-Hospiz 2310 m, 1948 v.S. (h); Piz Padella, 1915 Branger (Z); Las Trais Fluors, 1937 la Nicca (CHUR); also 2740 m, 1957 Lüdi (RUEB); Val Curtins, Oberhalbstein, 1914 Schinz (Z); Lunghino

pass 2400 m, v. Tavel (ZT); Rätschenfluh near St. Antonien, 1919 Baumgartner (ZT); Arosa, Rothorn 2400 m, Schröter (ZT); Parsenn 1900–2100 m, 1954 v.S. (h); Calanda, above 1800 m, Salèz (ZT); Sulzfluh, Rätikon 2100 m, 1952 v. Hattum & v. Ooststroom (h).

Oetztaler Alp.: Prossental 21–2400 m, on several spots, 1956 v.S. (h).

Salzburger Kalkalp.: Schneeberg, 1887 Faimann (W); Geisstein, Traunsteiner (W).

Sarntaler Alp.: Sarnerscharte 2400 m, Haussmann (W).

Stubaier Alp.: Gschnitztal, Trins, 1873 Churchill (K).

Brenner: Gries, 1865 Huter (K).

Hohe Tauern: Virgen 2400 m, 1866 Gander (K); Steiner Alpe near Windisch Matrei 2400 m, 1880 Mordnetz (W) and 1931 H.M. (W); Glockner region, 1905 Vierhapper (W); Teischnitz, Finsteres Tal 2600 m, 1953 Melzer (h); Gross Glockner, Franz Josefshöhe 2420 m, Mallnitzer Tauerntal, slopes of Feldseekopf and of Geiselkopf 1900 2000 m, Dössenertal nearby the lake 2250–2300 m, all 1957 v.S. (h); Hagener Hütte and Greilkopf 22–2500 m, 1932 H.M. (W).

Totes Gebirge: Tragln, Sigistal, 1952 Schaeftlein (h).

Karawanken: Hochobir near Kappel 1800 m, 1880 Preissmann (W).

Karnische Alp.: Cellonkofel 1600 m, 1957 Melzer (h).

Herzegovina: Trinaue, Płeša pl., Schneider (W).

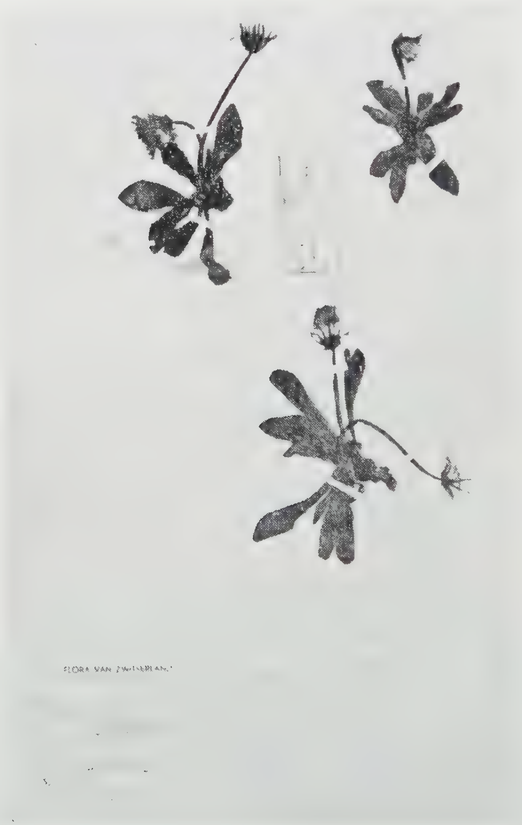

Fig. 2. T. helveticum v.S., type specimen.

3. **Taraxacum helveticum** van Soest **nov. spec.,** Fig. 2.

Planta 5–12 cm alta sat robusta, glabra vel valde glabrescens, basi fragmentis foliorum vetustorum subincrassata.

Folia numerosa subdecumbentia pallide vel luteo-viridia, lingulata vel subovata obtusa 1–2 cm lata, 3–9 cm longa, petiolis subnullis pallide viridis saepe latissime alatis; folia saepe integra vel retroverso-denticulata vel paulo breve triangulariter dentata.

Scapi 1–2(–4) subcrassi, florendi tempore foliis ± superantes, purpurascentes.

Involucrum mediocre ca. 15 mm longum, 10–15 mm latum, basi rotundatum, obscure viride. Squamae exteriores adpressae vel laxe patentes, parvae, ad 5 mm longae, ad 2,2 mm latae, ovatae acuminatae vel lanceolatae, omnes obtusae, saepe rufescentes, immarginatae laeves; squamae interiores late lineares, late membranaceo-marginatae, laeves.

Calathium subradians ad 2,5 cm diametro, luteum; ligulae marginales planae extus stria cano- vel fusco-violacea notatae, saepe summis subnigrae. Antherae polliniferae; stylus (parte superiore) et stigmata obscura, siccis subnigra. Floret aestate.

Achenium pallide brunneo-stramineum, ca. 4 mm longum superne breve spinulosum ceterum laeve, in pyramiden conicam brevam subabrupte abiens; rostrum breve, ad 4 mm longum; pappus sordide albus, 5 mm longus.

E sectione Alpinorum Haglund.

Typus: Bernina-Hospiz, July 1929 v. Soest (h. 1937).

Furthermore:

Alp. Maritimes: Mt. Mounier, Sellavieille 2400 m, 1911 St. Yves (LAU).

Alp. de Savoie: Petit St. Bernard, 1885 Pellat (h); Lac de Taveneuse 1800 m, 1903 Briquet (G).

Walliser Alp.: Distelalp near Saas 2150–2250 m, Plattjen 24–2500 m, Tälliboden 23–2400 m, Almagelltal 2800–2850 m, all 1953 v.S. (h); Ofental 1880 m, Chenevard (G).

Berner Alp.: Bell Alp near Brieg, 1873 Joad (K); Faulhorn 1800 m, Kützing (L); Alp. de Morcles, La Vire-aux-Boeufs 2000 m, 1906 Wilczek (LAU).

Vierwaldstädter Alp.: Uri, Bamberger (WAG).

Rhaetische Alp.: Val di Rodo, Duana pass 2700 m, 1892 Volkart (Z); Avers, Cucal Nair 2500 m, 1895 v. Tavel (ZT); Val Saluver, 1885 who? (CHUR); Weissenstein 2050 m and Albula pass 21–2300 m, both 1948 v.S. (h); Schlappin near Klosters 1650 m, 1954 v.S. (h); Roggentälli 21–2200 m, 1912 Zoya (RUEB); Gredigsaelpli near Arosa 2300 m, 1938 Maillefer (LAU); Fluela 2250 m, 1917 and Wuosthorn, both Schibler (Z).

Bernina: Hospiz, 1930 W. Koch (ZT); Fuorcla Surlej 2665 m, 1897 Knetsch (Z); Bernina pass 2050–2250 m, 1948 v.S. (h); Lago della Scala 2050 m, 1868 Brügger (ZT); Lago Bianco 2220 m, 1905 Rübel & Schröter (RUEB); Val del Fain, 1899 Hegi (Z); Chalchagn 2900 m, 1907 Rübel (RUEB); Maloja-Fuorcla di Lunghino 23–2400 m, 1895 v. Tavel (ZT); Piz Lagalb 2500 m, 1906 Schröter (ZT).

Silvretta: Vernelatal 2000–2200 m, Fremdvereina 1950 m, Süsertal 2100 m, all 1954 v.S. (h); Hafentälli 21–2200 m, 1912 Zoya (RUEB); Gaschurn, Garneratal, 1912 Vetter (W).

Vorarlberg: Fasultal, Konstanzer Hütte, 1912 Vetter (W).

Ortler: Martelltal, Konzenlacke 2600 m, 1956 Pohl (h. v.S.).

Oetztaler Alp.: Prossental 22–2400 m, 1956 v.S. (h).
Brenner: Gossensass and Hühnerspiel, 1910 Vetter (W); Saxalpenwand 2300-2698 m, 1932 H.M. (W).
Zillertaler Alp.: between Kalk- und Rollspitze 2300 m, 1957 Melzer (h).
Hohe Tauern: Klein Zirknitztal, 1911 Vetter (W); Geiselkopf 1800–1900 m, 1957 v.S. (h); Magdalenental, 1874 Churchill (K).
Gurktaler Alp.: Zundernwand near Radenthein 2000 m, 1950 Schaeftlein; Rinseneck 2200 m, 1949 Höpflinger (h. Schaeftlein).
Tatra: Fünf Seen, 1917 Schneider (W).

This species has dark stigmas; the typical form has entire leaves, attenuated in a long petiole; it cannot be confused with *T. petiolulatum* (Huter) m, having paler coloured stigmas, narrow petioles and being more tender in all its parts.

Not always the leaves are entire; they can be more or less lobate, the endlobe then being fairly polygonal; generally, this form is found at other localities than the typical one.

f. **lobatum** van Soest **f. nov.**

Ab *T. helvetici* differt: foliis breve vel elongato-lobatis; lobi laterales integri vel dorso dentati; lobus terminalis saepe polygonius, obtusus vel subobtusus.

Typus: Silvretta: Vernelatal 2500 m, 20.7.1954 v. Soest (h. 33891).

Furthermore:

Alp. Maritimes: Mt. Monnier 2400 m, 1911 St. Yves (LAU).
Alp. Bergamasques: Val di Scalve 2500 m, 1911 Wilczek (LAU); Val Sérienna 2100 m, 1913 Chenevard (G).
Walliser Alp.: Distelalp near Saas 2150-2250 m and Plattjen 24–2500 m, 1953 v.S. (h).
Berner Alp.: Novaier Thäli, Lauenzughorn 2220 m, 1913 Noack (RUEB).
Churfirsten: Brisigipfel 2280 m, 1914 Vogt (Z); Hinterruck, 1910 E. Müller (Z).
Glarner Alp.: Weisstannen, Flysch 2200 m, 1942 W. Koch (ZT); Nüschenalp, 1878 Lehmann (ZT).
St. Gotthard: 1849 who? (ZT).
Tessiner Alp.: Wandfluhhorn 2600 m, 1903 Bär (Z); Passo Corombe 2320 m, Furri (RUEB); Poschiavo, 1880 Pozzi (ZT).
Rhaetische Alp.: Avers, Gletscherhorn 27–2800 m, 1895 v. Tavel (ZT); Albula pass 2300 m, 1878 Kaeser (Z); Klosters, 1905 Laisi (Z); Parsennfurka 22–2400 m, 1954 v.S. (h); Körbshorn 2645 m, 1893 and Wuosthorn, both Schibler (Z).
Bernina: Piz Minor 2900 m and Piz Stretta 2820 m, both 1907 Rübel (ERUB); Fuorcla Muragl 2600 m, 1911 Branger (RUEB).
Silvretta: Vernelatal 2200 m, 1918 Noach (U); in the same valley on several spots between 2000 and 2250 m and Süsertal 2100 m, both 1954 v.S. (h); Vermonttal, 1912 Vetter (W); Gaschurm, Garneratal, 1912 Vetter (W).
Ortler: Martelltal 2350 m, 1956 v.S. (h); Stillfserjoch 2600 m, Dolenz (GZU); St. Gertraud, Sulden 2100 m, 1907 Preissmann (W).
Hohe Tauern: Freiwand near Franz Josefshöhe, 1912 Dolenz (GZU); Geiselkopf 1900 m and Dössenertal 2100 m, 1957 v.S. (h).
Niedere Tauern: 1910 Schneider (W).

4. **Taraxacum mattmarkense** van Soest **nov. spec.,** Fig. 3.

Planta parva ca. 6–8 cm alta, inferne araneosa.

Folia tenera luteo-viridia, superne glabra, inferne glabrescens, ad 6 cm longa ad 2,5 cm lata, lobata vel interdum grosse obtuse

late dentata; petiolis alatis pallide viridis; lobi laterales utrinque 2–3; deltoidei vel late triangulares obtusi integri, interlobiis saepe subnullis; lobus terminalis deltoideus obtusus vel deltoideo-hastatus, integer, lobuli basis breves obtusi.

Scapi ad 4, parce, sub involucro dense araneosi.

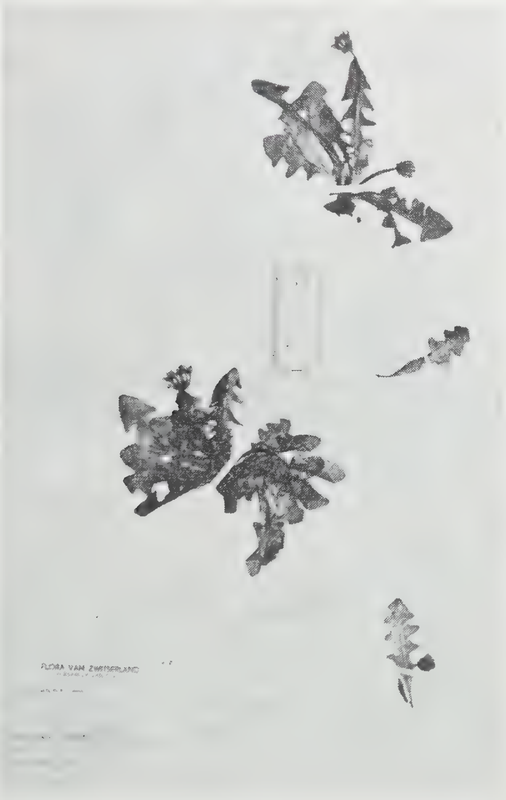

Fig. 3. T. mattmarkense v. S., type specimen.

Involucrum mediocre ca. 10 mm longum, ca. 10 mm latum; squamae exteriores laxe adpressae vel erecto-patentes lanceolatae ad 5 mm longae, ad 2 mm latae, late viride- vel roseolo-marginatae, apice obtusae purpureae; interiores late lineares membranaceo-marginatae conspicue ciliolatae, apice purpureae; omnes laeves.

Calathium paulo radians ad 17 mm diametro, clare luteum; ligulae marginales angustae subinvolutae estriatae summo aureo-purpureae. Antherae polline carentes; stylus et stigmata laete lutea; floret aestate.

Achenium maturum ignotum, pappus niveus.

E sectione Alpinorum Haglund.

Typus: Walliser Alp.: Saastal, near Mattmark 2100 m, 8.7.1952 v. Soest (h. 31090); furthermore in the immediate neighbourhood: on the same locality at 2150 m altitude; opposite the Allalin glacier, below Nollenhorn 2000–2100 m; Distelalp 2150–2250 m, all 1952 v. S. (h).

Furthermore:
Berner Alp.: Alpes de Bex, Paneyrossaz 2290 m, Villaret (LAU).

5. **Taraxacum oreophilum** Haglund, 1950. Ber. Schweiz. Bot. Ges. *60*: 238, c. icon.

This species is only mentioned from Piz Padella 2350 m in the Rhaetian Alps, 15.7.1938 W. Koch (S, ZT). It is closely allied to *T. panalpinumm*, but the lobes of the leaves are longer, the flower heads larger, the outer involucral bracts acute and not acuminate and, especially, the flowers are tubular, enclosing to a very high degree the anthers, the styles and the stigmas; the marginal flowers, at their outside, are bright purplish.

I have seen several alpine forms of *Taraxacum*, having more or less tubular flowers, no one, however, being identical with *T. oreophilum*. The achenes have a very short cone, showing that it belongs tc sect. *Alpina*; apart from the purplish outside, the flowers are dark yellow; confusion with species of sect. *Cucullata* m is therefore impossible.

6. **Taraxacum panalpinum** van Soest **nov. spec.,** Fig. 4.

Planta mediocris gracilis ca. 6 cm alta, basi fragmentis foliorum vetustorum subincrassata.

Folia ad 8 cm longa numerosa lobata luteo-viridia glabra, nervo mediano pallido raro parum rufescente, petiolis brevis pallide viridis raro parum roseolo-coloratis subalatis. Lobi laterales deltoidei vel saepissime triangulares summo saepe retroverso vel breve falcati dorso conspicue vel sub-convexo, interdum 1 dente parvo rare grosso munito, margine inferiore ± crispo-plicatulo. Lobus terminalis deltoideus vel subhastatus integer, acutus vel subacutus.

Scapi floriferi foliis aequilongi vel eis breviori, sub involucro araneosi vel interdum glabrescentes.

Involucrum mediocre 1,5 cm longum, 1,5 cm latum crassiusculum viride subglaucescens; squamae exteriores laxe adpressae apice recurvatae, ovatae vel ovato-lanceolatae saepe acuminatae (extremae angustiores), ultra ad 6 mm longae, 3 mm latae, apice obtusae, in superiore parte inconspicue marginatae vel immarginatae; squamae interiores late membranaceo-marginatae.

Calathium radians ad 2,5 cm diametro, obscure luteum; ligulae marginales planae angustae, extus stria rufo- vel cano-violacea notatae, summis saepe obscurae. Antherae vacuae vel paulo polliniferae; stylus superne sordide luteus, stigmata fusco-virescentia. Floret aestate.

Achenium ca. 4 mm longum (pyramide inclusa) rufo-stramineum, superne breviter spinulosum ceterum laeve, in pyramiden conicam

0,6 mm longam abrupte abiens. Rostrum breve, ad 6 mm longum; pappus albus, 6 mm longus.

E sectione Alpinorum Haglund.

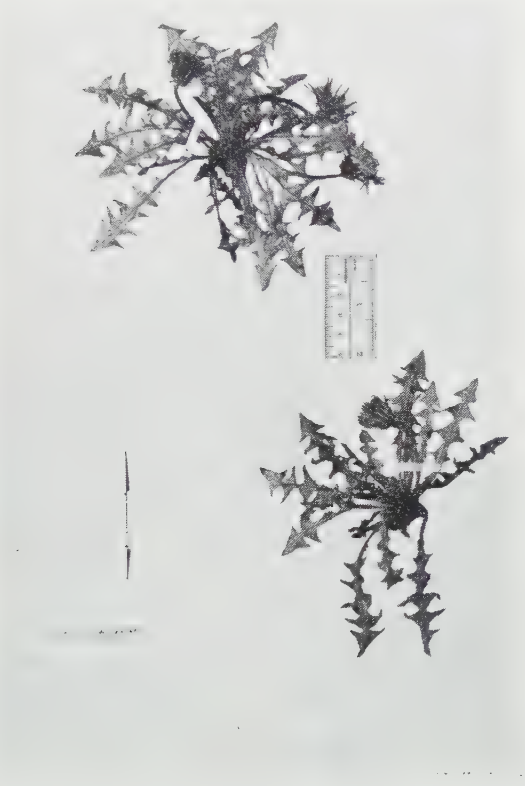

Fig. 4. T. panalpinum v.S., type specimen.

Furthermore:

Serra da Estrêla: Lagoa Comprida, 1881 Ferreira (COI).

Serra da Lousã: 1883, Henriques (COI), both considered by me as *T. alpinum* s.str. in Agronomia Lusitana 1951. *13.1.*

Sierra Nevada: Prado de Vedegambra 2600 m, 1923 Font-Quer & Gros (BC, h. v.S.).

Hautes Pyrenées: Lac d'Oredon 1870 m, 1949; Vallée d'Aussone, Gavarnie 1900m, 1952; lac d'Aumar 2193 m, 1952, all J. Aylies (h. de Litardière).

Hautes Alpes: Galibier, 1877 Pellat (h).

Mont Blanc: Mer de Glace 2780-2997 m, Venance Payot (G); Allée Blanche, 1863 Perrier (G); Pointe Ronde, near Martigny 2500 m, 1922 Farquet (ZT).

Alp. de Savoie: Col de Tanneverge 23–2500 m, 1902 Briquet (G); Col de Pelouse 2300 m, 1949 A. H. Palm-Lyesen (U); Hauteluce, 1865 Perrier, exsicc. Billot (GZU); Pic de la Vogéalle 2600 m, 1893 Briquet (G); between Aiguille de Varens and Tête de Colleney, 1902 Briquet (G).

Walliser Alp.: St. Bernard 2450 m, 1910 and 1921; Hospice 1893 and 1923, all Wilczek (LAU); Alpes de Fulley, 1877 Burdet (LAU); Vallon de la Toula — Col Coudarche 2600 m, 1910 Wilczek (LAU); Zermatt, Riffel 1870 Favrat (LAU); 1879 Hooker (K) and 1922 Thellung (Z); Gornergrat, 1907 Rohrer (Z) and 1910 Western (K); also 3100 m and Hörnli 2850 m, both 1919 Thellung (Z); Schönhorn 2246 m, 1904 Knetsch (Z); Pas de Forcletta, between Val de Zinal and Turtmanntal, 1897 Knetsch (Z); Simplon, Kaldwasser (G); Saastal, Distelalp 2150–2250 m, Gletscheralp near Saas-Fée 23–2400 m and Almagelltal 26–2800 m, all 1952 v.S. (h).

Berner Alp.: Vallée de l'Etivaz, Laudallaz 1995 m, 1943 Maillefer (LAU); Faulhorn, 1891 Chenevard (G) and also 2618–2683 m, 1841 Martins & Bravais (G); also 2672 m, 1921 Blauer (Z); Paneyrossaz 1800 m, 1866 Thomas (K); Melchsee — Frutt, Blausee, 1938 Wallimann (ZT); Brienzer Rothorn, 1931 Blauer (Z); Eigergletscher 2340 m, 1918 Michalski (Z); Gemmipass, S. Fries (Z).

Vierwaldstädter Alp.: Fellital 2600 m, 1915 Schmid (Z).

Glarner Alp.: Fridolinshütte near Tödi, 1902 Thellung (Z); Maderanertal, Alpli 2400 m, 1915 Schmid (Z).

Appenzeller Alp.: Säntis, Alpsiegel 1640 m, 1918 Koller (Z).

Tessiner Alp.: Furka, Marschenspitz Bosco, 1903 Bär (Z); Val Onsermone near Comologno, 1905 Bär (Z); Passo Corombe 2320 m, Furri (RUEB).

St. Gotthard: 1849 who? (ZT).

Rhaetische Alp.: Piz Beverin 21–2400 m, 1869 Brügger (ZT); Albula pass 21–2300 m, 1948 v.S. (h); Piz Saluver 2800 m, 1904 Candrian (Z); St. Moritzer Alp, Imhoof (LAU); Urdenfurkli 2620 m, 1920 Beger (Z); Oberhalbstein, Val Curtegns, 1918 Schinz (Z); Strela 2653 m, 1893 Schibler (Z); Strela Alp, 1924 Givardet (LAU); Val Nuglia 2600 m, 1920 Wilczek (LAU); Ducanpass, Sertig-Davos 2671 m, 1893 Schibler (Z); Körbshorn 2645 m, 1893 Schibler (Z).

Bernina: Hospiz 2300 m and pass 2050–2250 m, both v.S. (h); Cambrena 2400 m, 1904 de Litardière (k); Val Minor 2300 m, 1905 Rübel & Schröter (RUEB); Piz Chatscheders — Piz Stretta 2780 m, 1907 Rübel (RUEB); Maloja, 1899 Hegi (Z); Piz Languard 3000 m, 1953 Duvigneau (h); Lagalbsee 2400 m, 1905 Braun & Rübel (RUEB).

Silvretta: Seetal 2000–2050 m, Süsertal 2100 m, Alp Sardasca 1650 m and Vernelatal 2100 m, all 1954 v.S. (h); Klosters, Hafentälli 21–2200 m, 1917 Zoya (RUEB); Galtür, 1927 Schneider (W).

Lechtaler Alp.: Rüfikopf near Lech 2350 m, 1958 Damblon (h. Lambinon).

Ortler: Martelltal, Zufallhütte 2200 m, 1900 Dolenz (GZU); in this valley on several spots 2000–2350 m, 1956 v.S. (h); Plattkogl, 1876 Stein (G).

Oetztaler Alp.: Prossental 22–2600 m, 1956 v.S. (h); Sölden, 1901 Kerner (GZU); Samoar Hütte, 1906 Korb (W).

Brenner: Rollspitze, north slope 2200 m, 1953 Schaeftlein (h); Hühnerspiel, who? (GZU) and 1886, Evers (GZU).

N. Tiroler Alp.: Hafelekar 2100 m, 1882 Evers (GZU).

Zillertaler Alp.: Weissenbach 24–2700 m, Treffer (GZU), also 2000–2500 m, 1880 Treffer (Gr.).

Sanntaler Alp.: Sanntaler Sattel and Kankersattel, both 1931 Korb (W).

Hohe Tauern: Windtal near Lenkjöchel, Venediger 2400 m, 1906 Dolenz (GZU); Mallnitzer Tauern 2300 m, 1904 Dolenz (GZU).

Niedere Tauern: Judenburger Alp., Fenzl. (W).

Totes Geb.: Tragln, Sigital, 1952 Schaeftlein (h).

Eisenerzer Alp.: Admont, Speckmover (W).

Tatra: Lomnitzerspitze, Láng (W).

Transsilvanische Alp.: Pareng, 1883 Barth (W).

Albania: Kom. Kuči, Iter Mont. 1886 de Szyszyłowicz (W); Dibala, Iter Alban. Sextum Baldacci 226, 1898 (G, K, W).

From a taxonomical point of view this species occupies the central place in the field of characteristics within the section; it also seems to have the largest area and to be the most common of all species of this spection. Still it is impossible to consider it as the true *T. alpinum* as described by Hoppe (as *Leontodon*) or by Hegetschweiler & Heer, as I did in a few earlier studies.

In Sturm 1821, Deutschlands Flora 5, *Leontodon alpinus* Hoppe is pictured; with the exception of two leaves below it seems to represent *T. panalpinum*; three localities are mentioned in this Flora (Heiligenbluth, Salmhöhe, Gamsgrube); these, however, do not appear in the list given above. From Heiligenbluth I know: *T. kalbfussii*, from Salmhöhe: *T. venustum* and *T. petiolulatum*, all collected by Hoppe; from Gamsgrube I know material from *T. vetteri*, collected in 1904 by Vetter.

T. panalpinum shows more variability than most other species of the section; splitting up this species in smaller groups does not seem practical to me. Pollen is present, but some times more or less absent; the stigmas are dirty yellow, often greenish yellow; the scapes of the flower heads are hairy at the top, but some times glabrous; the leaves are yellowish green and have mostly recurved triangular lobes. The dark green outer involucral bracts are more or less spreading, often with recurved apex. The achenes are typical for the *Alpina*, having a short cone and a short rostrum.

With ripe achenes no confusion is possible with *T. rhaeticum* m (sect. *Vulgaria* Dahlst.); this one has a long rostrum, nearly twice the length of the achenes; without achenes a decision whether the form in study is *T. panalpinum* or a small specimen of *T. rhaeticum* is more difficult. The leaves of *T. rhaeticum*, however, are greyish to grass-green; the involucres are not so dark and the stigmas are more pure yellow.

T. carinthiacum m is allied to *T. panalpinum*, but the difference in shape of the leaves and their lobes makes a decision whether a specimen belongs to the one or the other not difficult.

7. **Taraxacum parsennense** van Soest **nov. spec.,** Fig. 5.

Planta mediocris ca. 6–10 cm alta, subglabra.

Folia subnemorosa gramineo-viridia, petiolis subalatis — alatis pallidis vel rufescentis. Folia interiora lobata; lobi laterales utrinque 2–3, triangulares summo acuto saepe retroverso vel recurvo, integri raro 1 dente muniti, interlobiis ca. 5 mm latis interdum paulo denticulatis; lobus terminalis ad 2,5 cm longus hastatus saepe indeterminato-sublobatus vel 1 dente retroverso grosso munitus, subobtusus.

Scapi floriferi foliis aequilongi, sub involucro subaraneosi.

Involucrum mediocre basi ovatum, atroviride. Squamae exteriores laxe patentes apice recurvatae, ovato-lanceolatae ad 7 mm longae immarginatae, saepe purpurascentes. Squamae interiores late lineares, 12 mm longae.

Calathium planum radians ca. 3,5 cm diametro, obscure luteum. Ligulae marginales planae, extus estriatae vel inconspicue canostriatae, summo ± nigro. Antherae polliniferae; stylus inferne luteus, sordide luteus; stigmata obscure fusco-lutescentia.

Achenium maturum ignotum stramineum, superne (breve?) spinulosum, ceterum ± laeve, in pyramiden conicam sensim abiens; rostrum achenio ad duplo longius?; pappus albus.

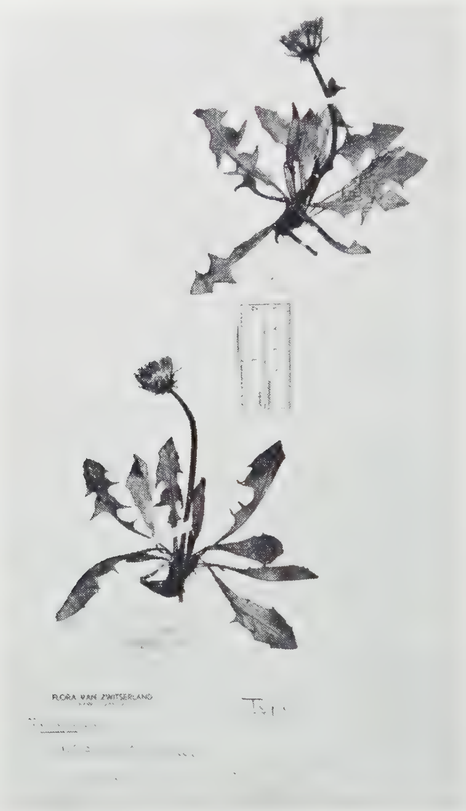

Fig. 5. T. parsennense v.S., type specimen.

Typus: Rhaetische Alp.: Parsenn near Klosters, between 1900 and 2400 m, 21.7.154 v. Soest (h. 33859).

Furthermore:

Glarner Alp.: Maderanertal, Schwarzstöckli, 1915 Schmid (Z).
Rhaetische Alp.: Dischatal near Davos, 1907 Bär (Z); Schlinigtal 1800 m, 1956, v.S. (h).

This species, though very probably belonging to section *Alpina*, is related to the *Vulgaria* Dahlst.: the rostrum seems to be relatively long and also the habit shows some resemblance to mountaineous species of *Vulgaria*. Often the leaves of *T. parsennense* have brownish petioles, a characteristic not common in *Alpina*. The ligules are more or less lacking coloured stripes.

8. **Taraxacum petiolulatum** (Huter) van Soest **nov. comb.**; *T. officinale* var. *petiolulatum* Huter, in sched. 21.8.1878; *T. alpinum* var. *glabrum* von Handel–Mazeztti, 1907. Monogr. Tarax.: 94, c. icon: V. 10d, non *T. glabrum* De Candolle, 1838; *T. officinale* ssp. *alpinum* var. *glabrum* Hegi 1928. Fl. Mitt. Eur. *6.2:* 1092.

The description given by Huter is very short: "foliis aperte petiolulatis, ovatis subintegris, floribus croceis"; nevertheless it is, if applied to the section *Alpina* Hagl., a nearly sufficient one. According to modern principles in the description of *Taraxacum* species, a more complete one is needed, following below. In his monography H.M. has published a photographic reproduction of var. *glabrum*, being, according to him, identical with *T. glabrum* DC. and with *T. petiolulatum. T. glabrum* DC., however, is a very different species, belonging to sect. *Glabra* Dahlst. and only represented in the arctic region. Though from a descriptive point of view the name "petiolulatum" better had to be changed in "petiolatum", I do not change it for nomenclatoral reason.

Planta gracilis 7–10 cm alta subglabrescens, collum radicis araneosum.

Folia supra glabra subrotundata vel elliptica vel obovata, obtusa integra, ± dentata vel raro pro parte sublobata, in petiolis pallide viridis 1–3(–4) cm longis breve vel sublonge truncata.

Scapus glabrus.

Involucrum ca. 11 mm longum. Squamae exteriores laxe adpressae parvae sublineares vel pro parte sublatiores ad 3 mm longae obtusae immarginatae pallide virides, interiores subobscure virides late marginatae, omnes laeves.

Calathium subradians ad 2 cm diametro, croceum. Ligulae marginales planae, extus stria cano-purpurea ornatae; antherae polliniferae; stylus et stigmata sordide lutea; floret aestate.

Achenia matura ignota, pappus niveus.

E sectione Alpinorum Haglund.

Typus Huterianus: Pusteria, Sexten (Tirol), brevissime graminos. aqua nivali irrigati in Givenglabl, sol. calc., 2300 m, 21.8.1878 Huter (W. 1889/5138 4); also in herb. K.

Furthermore:

Silvretta: Garneratal, Gaschurn, 1912 Vetter (W).
Rhaetische Alp.: Schlinigtal 1800 m, 1956 v.S. (h).
Ortler: Martelltal 2350 m, 1956 v.S. (h).
Lechtaler Alp.: 2300 m, 1930 Wyatt (K).
Oetztaler Alp.: Prossental 21–2600 m, 1956 v.S. (h).
Stubaier Alp.: Gschnitz, see H.M. l.c. fig. 10 d.
Brenner: Tierser Alp — Seiser Alpenhaus, 1912 Vetter (W); Steineralpe near Matrei 2400 m, 1931 H.M. (W); Matrei, A. Kerner (BR).
Zillertaler Alp.: Tristental 2000–2500 m, 1880 Treffer (GR); in the same valley 22–2600 m, 1887 and 1888 Treffer (LAU, ZT).
Defereggen Alp.: Bahlenke, 1929 Schneider (W).
Gailtaler Alp.: Laserzwand, 1929 Gayer (GZU).
Hohe Tauern: Feldseekopf 19–2000 m and Geiselkopf 1900 m, 1957 v.S. (h); Glockner, 1905 Vierhapper (W); Salmhöhe, Hoppe (L).

Karnische Alp.: Upper Valentin 2200 m, 1934 Schaeftlein (h); Pustertal, 1878 Huter (K).
Dolomiten: Passo di Pordoi 2200 m, 1955 Keuchenius (U); Schlern 2450 m, 1954 Melzer (h).

This species has an eastern alpine area; no locality from Switzerland is known, though it reaches the border of this country.

9. **Taraxacum pseudofontanum** van Soest **nov. spec.**, Fig. 6.

Planta mediocris gracilis 5–15 cm alta, basi subglabra.

Folia lingulata luteo-viridia vel gramineo-viridia, parce, in nervo dorsali interdum ± rufescente conspicue araneosa; petiolis ± alatis pallide viridis. Folia exteriora dentata; interiora lobata vel lobulato-

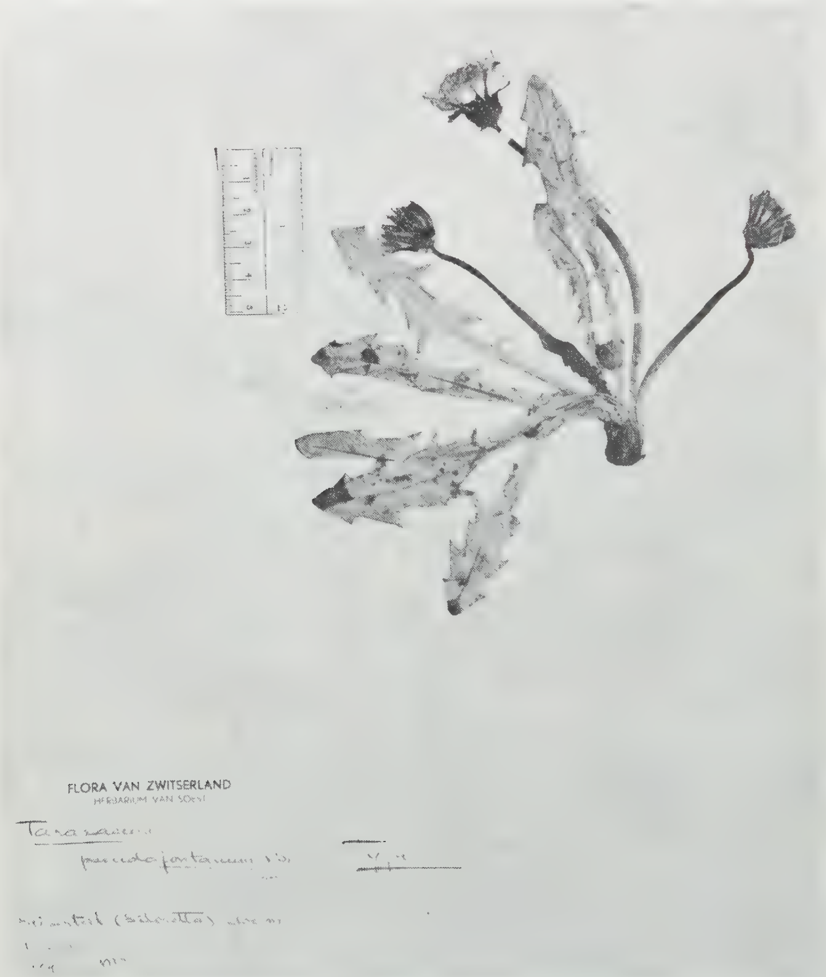

Fig. 6. T. pseudofontanum v.S., type specimen.

dentata, ca. 6 cm longa, ad 1,8 cm lata, subobtusa; lobi laterales utrinque ca. 3, breves, triangulares vel lanceolati vel subunguiculati ± retroversi denticulati vel dorso 1 dente muniti.

Scapi 1–4, foliis aequilongi vel eis breviter superantes, sub involucro araneosi vel subglabri.

Involucrum mediocre 15 mm longum, 12–14 mm latum, viride. Squamae exteriores apice ± recurvatae, lanceolatae ad 8 mm longae 1,5 mm latae apice elongatae, pallide virides, ± anguste albo- vel virescenti- marginatae; squamae interiores late lineares apice ± purpureae.

Calathium subradians vel radians ad 3 cm diametro, saturate luteum. Ligulae marginales extus stria cano-purpurea notatae apice subnigrae. Antherae polliniferae; stylus et stigmata clare lutea. Floret aestate.

Achenium stramineum 3,5 mm longum (pyramide exclusa) superne brevissime spinulosum ceterum laeve, in pyramiden 0,5 mm longam inconspicue abiens. Rostrum 5–6 mm longum, pappus 5 mm longus.

E sectione Alpinorum Haglund.

Typus: Oetztaler Alp.: Prossental 21–2200 m, 18.7.1956 v. Soest (h. 36731, 36752); in the same valley this species is collected abundantly up to 2400 m, 1956 v. S. (h).

Furthermore:

Walliser Alp.: Almagelltal 26–2800 m, 1952 v.S. (h).
Glarner Alp.: Widerstein Furkel 18–2000 m, 1910 Roth (Z).
Rhaetische Alp.: Val Bregalga, Avers 2000 m, 1938; Palpuogna, Albula 1900 m, 1948, both v.S. (h); Fideris, Glunersee, Flütsch (CHUR); Schlappin near Klosters 1650 m and Parsenhütte 2200 m, both 1954 v.S. (h).
Bernina: Berninatal 2050–2250 m, 1948 v.S.(h); Fuorcla Surlej 23–2700 m, 1905 Rübel (RUEB).
Silvretta: Hafentälli 21-2200 m, 1912 and Vernelatal 2000 m, 1913 Zoya (RUEB); Vernelabach near Vereinahaus 1950 m, Vernelatal 2000-2200 m, Alp Sardasco 1650 m, Süsertal 2100 m, all v.S. (h); Gross Vermunt 2000 m, 1951 Melzer (h).
Oetztaler Alp.: Prossental 2400 m, 1956 v.S. (h).
Ortler: Martelltal 2350 m, 1956 v.S. (h).
Brenner: Gries, 1865 Huter (K).
Dolomiten: Schlern, Schneider (W); Passo di Pordoi 2300 m, 1955 Keuchenius (U).
Hohe Tauern: Mallnitzer Tauerntal, below Geiselkopf 1900 m, Dössenertal 2000 m, and near Dössenersee 2250–2300 m, all 1957 v.S. (h).

This species is closely related to *T. helveticum* m; it can easily be recognized by its clear yellow stigmas, which are dark grey in *T. helveticum*. Furthermore, the pale outer involucral bracts, generally with recurved apex, are remarkable. In leaf form there is a striking resemblance to species of sect. *Fontana* m, such as *T. fontanicolum* m, having a longer rostrum and dentate leaves, with dents not directed backward in general.

10. **Taraxacum saasense** van Soest **nov. spec.,** Fig. 7.

Planta ad 10 cm alta subglabra.

Folia numerosa conspicue tenera luteo-viridia glabra, petiolis subalatis vel alatis pallide viridis; folia exteriora oblanceolata integra vel sublobata; folia interiora lobata; lobi laterales utrinque ca. 3, breve deltoidei vel triangulares summo acuminato subobtuso, integri, inferne raro ± dentati; interlobiis subnullis 3–10 cm latus raro dentatis; lobus terminalis saepe breve deltoideus subobtusus saepe apice mucronatus, interdum indeterminato-sublobatus vel dentatus.

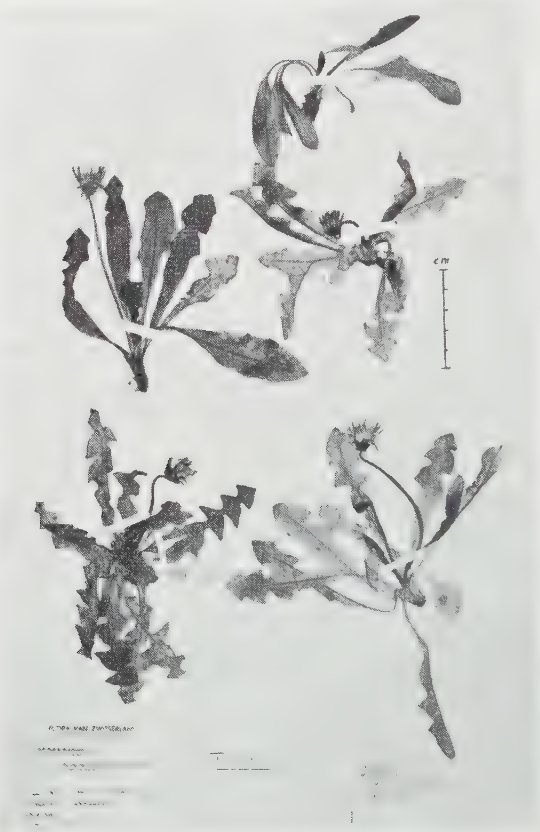

Fig. 7. T. saasense v.S., type specimen.

Scapi 1–2, sub involucro parcissime araneosi vel glabri, basin versus parce araneosi.

Involucrum subparvum ca. 10 mm latum, 12 mm longum. Squamae exteriores laxe adpressae parvae lanceolatae, ad 5 mm longae, pallide virides, apice violaceae; squamae interiores obscure virides, late lineares membranaceo-marginatae, omnes laeves.

Calathium paulo radians ad 2 cm diametro, luteum. Ligulae marginales planae extus stria obscure rubro-violacea notatae, summis subnigrae. Antherae (parce?) polliniferae; stylus parte inferiore clare luteus, superne obscurus; stigmata obscura, siccis subnigra. Floret aestate.

Achenium dilute brunneum, maturum ignotum, rostrum achenio subaequilongium, pappus albus.

E sectione Alpinorum Haglund.

Typus: Walliser Alp.: Saas–Fée, above the Gletscher Alp 23–2400 m, 23.7.1952 v. Soest (h. 31073–4); furthermore in the neighbourhood: Plattjen 24–2500 m, Mattmark 2100–2150 m, both 1952 v. S. (h); Plattjen, 1919 Arnow (Z).

Furthermore:

Alp. Maritimes: Tenda, near Lacum di Fontanalba, 1911 Bicknell & Pollini, Fl. Ital. exsicc. II. 1996 Fiori & Béguinot (K, LAU, ZT).
Alp. de Savoie: Col de Bix, 1903 Briquet (G).
Walliser Alp.: Simplon, 1865 Bader (G).
Berner Alp.: Alp. de Bex, Vallée de l'Avançon d'Anzeindaz 2085 m, 1943 Villaret (LAU).

This species, belonging to the West-alpine Flora, is easily recognized by its thin and yellowish green leaves with very short deltoid lobes; the outer involucral bracts are small and pale green, the stigmas are dark coloured.

11. **Taraxacum vereinense** van Soest **nov. spec.,** Fig. 8.

Planta gracilis 7–10 cm alta glabrescens.

Folia laete gramineo-viridia ca. 10 cm longa (petiolis angustis vel subangustis pallide viridis inclusa) profunde lobata; lobi laterales utrinque 3–4, angusti, triangulares vel falcati, dorso longe anguste dentati, margine inferiore integro, interlobiis dentatis sublongis 2–3(–5) mm latis; lobus terminalis subacutus, lobuli basis acuti.

Scapi 1–2 graciles, sub involucro saepe araneosi.

Involucrum ca. 11 mm longum, 12 mm latum, atro-viride; squamae exteriores erecto-patentes apice recurvatae, lanceolatae ca. 7 mm longae subacutae vel subobtusae, angustissime albo- vel pallide purpureo-marginatae; squamae interiores membranaceo-marginatae.

Calathium paulo radians ad 17 mm diametro, obscure luteum; ligulae marginales planae extus stria cano-purpurea ornatae; antherae parce polliniferae; stylus inferne luteus, superne virescenti-luteus; stigmata virescenti-lutea; floret aestate.

Achenium dilute brunneum 3 mm longum (pyramide exclusa) superne spinulosum ceterum rugosum—basi laeve, in pyramiden conicam 0,5 mm longam subabrupte abiens; rostrum 6–7 mm longum; pappus albus, 5 mm longus.

Typus: Silvretta: Vereinahaus 1950 m, 18.7.1954 v. Soest (h. 33810).

Furthermore:

Walliser Alp.: Hannigalp near Saas-Fée 22–2400 m and below Mittaghorn 1800 m, both 1952 v.S. (h).
Rhaetische Alp.: Albula pass 21–2300 m, 1948 v.S. (h); Piz Padella 2200 m, 1910 Branger (RUEB); Oberhalbstein, Piz Curver 2435 m, Schröter (RUEB).
Silvretta: Vernelatal 2100 m, 1954 v.S. (h).
Ortler: Martelltal 2250 m, 1956 v.S. (h).
Oetztaler Alp.: Prossental 21–2200 m, 1956 v.S. (h).

T. vereinense has a rather long rostrum, which makes it uncertain if this species belongs to sect. *Alpina*. The habit of the plant, however, is alike those of species of this section. On the other hand it seems to flower a little bit earlier than the others and also the achenes ripen earlier. There is some resemblance to small forms of *T. rhaeticum* m (sect. *Vulgaria* Dahlst.), but this species lacks pollen and has pure yellow stigmas, as well as *T. perfissum* m.

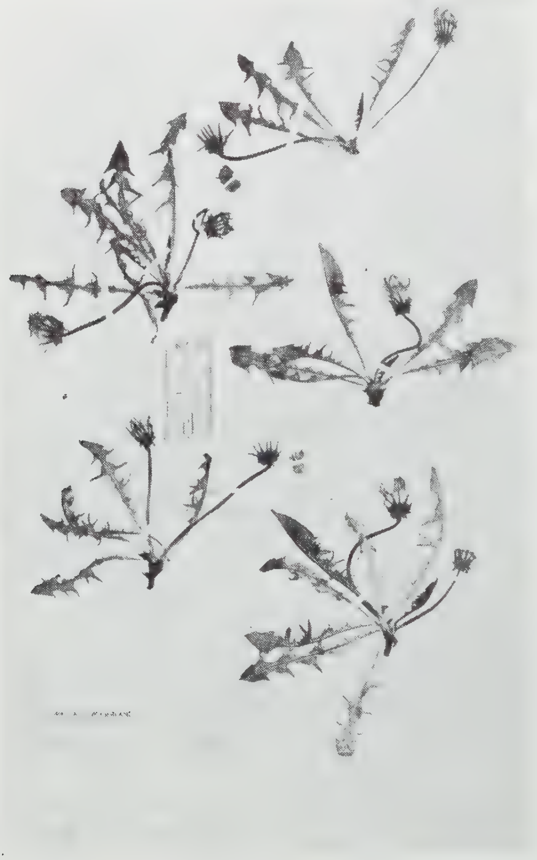

Fig. 8. T. vereinense v.S., type specimen.

12. **Taraxacum venustum** Dahlstedt 1908. Arkiv f. Bot. *7.1*: 5, non Koidzumi 1933 Bot. Mag. Tokyo: 104; *T. officinale b. Kalbfussii* Schultz–Bip. 1933. Flora *16.2*: 605; von Handel–Mazzetti 1907. Monogr. Tarax.: 94; *T. alpinum var. Kalbfussii* Sch.–Bip. in Braun–Blanquet & Rübel 1936. Fl. Graubunden: 1476; *T. officinale ssp. alpinum var. Kalbfussii* Hegi 1928, Fl. Mittel-Europa *6.2*: 1092; *T. alpinum var. hyoseridifolia* Baer & Hellweger in Herb. norm. Dörfler

1899 (no. 4063), non *T. hyoseridifolium* Arvet–Touvet & Marcou d'Aymeric 1892.

The descriptions given by Baer and Hellweger, and by Schultz–Bip.—the latter being clear and accurate—needed addition, given by Dahlstedt. The name *T. venustum* and its description are hidden in a short note at the foot of page 5; therefore I used earlier the (older) name *kalbfussii* during the revision in several herbaria. As lectotype we have to choose Dörflers exsiccatum from Hühnerspiel, see below.

This species is only known from the east alpine region, where it is common at an altitude from (1700–)2000–2700 m above sea level.

Algäuer Alp.: Nebelhorn, Bornmüller (S).
Rhaetische Alp.: Piz Uertsch 2500 m, Schröter (ZT); Val Maisas 2600 m, 1867 Favrat (LAU) and 1906 Sulger Buel (Z); Samnaun, 1856 Krättli (Z) and 1867 Favrat (LAU); Davos, Grosse Schiahorn 2700 m, v. Tavel (ZT); Ducan pass, Sertig 2671 m, 1893 Schibler (Z); Fimberjoch, Jaeggi (ZT).
Bernina: Piz Alv and Val Minor 2300 m, both Rübel & Schröter (RUEB); Piz Alv, who? (AMD); Piz Canciano, Pozzi (ZT); Piz Lagalb 2500 m, 1906 Schröter (ZT).
Silvretta: Vernelatal 2000–2250 m, on several spots, 1956 v.S. (h).
Lechtaler Alp.: Rüfikopf near Lech 2350 m, 1958 Damblon (h. Lambinon).
Ortler: Martelltal 2100–2350 m, on several spots, 1956 v.S. (h); Konzenlacke 2600 m, 1956 Pohl (h. v.S.); Edelweisshütte near Trafoi, 1913 Vetter (W); St. Gertraud, Suldental 2100 and 2700 m, 1906 Preissmann (W).
Brenta Alp.: Cima Val Skura 2000–2200 m, 1918 R. Czegka (GZU).
Stubaier Alp.: Trins and Naturfreundehaus, Padaster, both 1930 Korb (W); Padasterjoch, 1910 Schneider (W); Gschnitztal, Churchill (K), for this valley see also H.M., Monogr. fig. 10 b; Muttenjoch 2700 m, 1873 (K).
Brenner: Sterzing, 1912 Glowacki (GZU); Hühnerspiel near Gossensass 2400–2730 m, 1899 Bear & Hellweger, exsicc. Dörfler no. 4063 (G, GZU, LAU, O, P, RUEB, S, W); Hühnerspiel, 1910 Vetter (W) and 1953 Schaeftlein (h); Wolfendorn, 1912 Vetter (W).
Zillertaler Alp.: Tristen 24–2700 m, Treffer (GZU); Rohrbach, St. Johann 2000–2400 m, Treffer (W).
Hohe Tauern: Venedigergruppe, Lenkjöchel 2400 m, 1906 Dolenz (GZU); Umbal, Prägraten, 1913 Schneider (W), with a sketch of the achenes!; Knappenhaus, 1915 Korb (W); Sonnblickgebirge, Würthen, 1929 Schneider (W); Fuschertörl, 1931 Schneider (W); Waschgangalpe, Sagritz, exsicc. Schulz–Bip. 74, Pacher (K, L. O. S); Salmhöhe, Hoppe (L); Heiligenbluth, Hoppe (K); and Hallender 1914 (W); also 2400 m, 1885 Freyn (h. de Litardière); Heiligenbluth-Sagritz, Lagger (LAU); Franz Josefshöhe, Pasterze 2330 m, 1880 Preissmann (W); Ködnitztal 2750 m, 1953 Melzer (h); Goldberggruppe, Stellkopf, 1935 Widder (h), Leitertal, 1905 Vierhapper (W); Gross Glockner, Kokeil (K); Böseck, Mallnitzer Tauerntal 1700 m and Dössenersee 2250–2300 m, 1957 v.S. (h); Hagener Hütte and Greilkopf, 1932 H.M. (W).
Karnische Alp.: Pustertal 18–2400 m, 1867 Ausserdorffer (K).
Dachsteingebirge: Adamekhütte, 1924 Korb (W); Edelgrieshöhe 2200 m, 1941 Schaeftlein (h).
Eisenerzer Alp.: Admont, Speckmover (W); Kalbling 1800 m, Kock (L, P).

Probably I saw this species also from Transsilvania, C. Getz (L). Braun–Blanquet & Rübel l.c. have mentioned five localities from the Bernina region and one from the other Rhaetian Alps.

13. **Taraxacum vernelense** van Soest **nov. spec.,** Fig. 9.

Planta mediocris 8–9 cm alta subglabra, basi fragmentis foliorum vetustorum incrassata.

Folia subdecumbentia luteo-viridia vel gramineo-viridia glabra, petiolis angustis nervoque mediano pallide viridis, exteriora obovata in inferiore parte dentata vel sublobata. Folia interiora 5–6 cm longa, lobata; lobi laterales utrinque 2–3 parvi breves triangulares vel deltoidei, integri obtusi vel subacuti vel inferiores acuti, interlobiis subangustis vel latiusculis integris; lobus terminalis sat magnus saepe $^1/_2$–$^1/_3$ totae foliae longus, ad 2–3 cm longus ± hastatus obtusus integer vel raro minute dentatus vel subincisus, lobuli basis paulo evoluti.

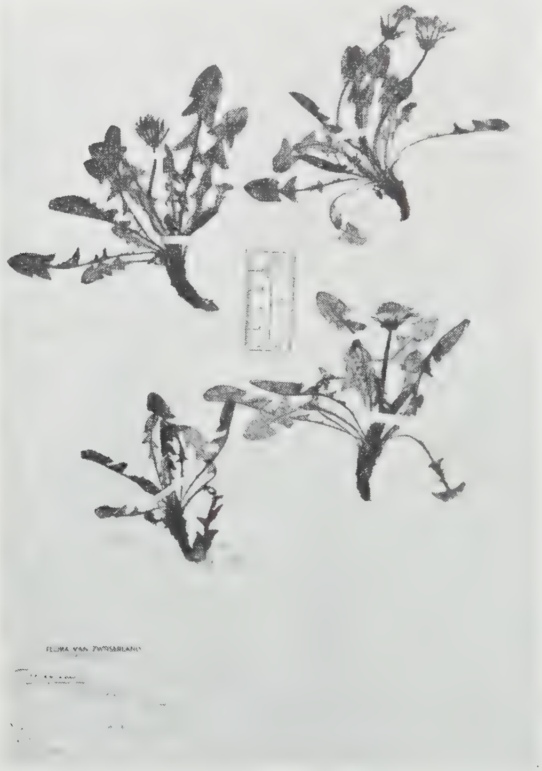

Fig. 9. T. vernelense v.S., type specimen.

Scapi 1–2, sub involucro parce araneosi vel glabrescentes.

Involucrum mediocre, obscure viride; squamae exteriores laxe adpressae apice recurvatae, lineari-lanceolatae 4–6 mm longae, inferne 1,5 mm, superne 0,5 mm latae, obtusae inconspicue sublate pallido-marginatae, brunnescentes laeves. Squamae interiores lineares, membranaceo-marginatae laeves.

Calathium radians ad 3 cm diametro luteum; ligulae marginales ± involutae vel angustae extus stria atro-violacea notatae, summis subnigrae. Antherae polliniferae; stylus et stigmata subobscura; floret aestate.

Achenium ochraceum 3,5 mm longum (pyramide inclusa) superne minute spinulosum vel tuberculatum ceterum laeve, in pyramiden conicam 0,3 mm longam subsensim abiens; rostrum ad 3 mm longum, pappus albus 5 mm longus.

E sectione Alpinorum Haglund.

Typus: Silvretta: Vernelatal 2050 m, 18.7.1954 v. Soest (h. 33878–80).

Furthermore:

Rhaetische Alp.: Parsennhütte near Klosters 2200 m, 1954 v.S. (h).
Tessiner Alp.: Alpe Motto — Pizzo Scaglie, Val Verzasca 1900 m, 1903 Jaggli (G).
Bergamasker Alp.: Monte Legnone — Lagho Delegnaccio 2190 m, 1911 I. Braun (G).
Brenner: Vennatal, 1926 Vetter (W).
Hohe Tauern: Dössenersee 2250–2300 m, 1957, v.S. (h).

In its leaf form this species is alike *T. cucullatum* Dahlst., but the whole plant is smaller and the flower heads are deep yellow; *T. cucullatum* often grows in mowing fields in the alpine region, *T. vernelense* on the other hand prefers humid, short grassy slopes. The achenes of *T. vernelense* are characteristic for the section *Alpina*.

14. **Taraxacum vetteri** van Soest **nov. spec.,** Fig. 10.

Planta mediocris ad 12 cm alta subglabra.

Folia luteo-viridia, ad 9 cm longa, petiolis pallide viridis vel subroseolis anguste alatis inclusa; lobi laterales utrinque 3–4, breves deltoidei vel lingulati vel triangulares, ± breve dentati vel denticulati, summis saepe retroversi interdum erecto-patentes, interlobiis saepe grosse dentatis; lobus terminalis deltoideus vel deltoideo-hastatus subacutus, lobuli basis acuminati acuti.

Scapi sub involucro paulo araneosi.

Involucrum basi ovatum obscurum, siccis nigrum. Squamae exteriores laxe patentes ovato-lanceolatae ad 7 mm longae, 3 mm latae, angustissime marginatae, interdum ciliolatae; interiores 13–14 mm longae.

Calathium 1,5–2 cm diametro, paulo radians. Ligulae luteae, marginales involutae, extus roseolo- vel purpureo- vel pro parte e-striatae; styli lutei, stigmata ± sordide lutea, antherae vacuae. Floret aestate (augusto).

Achenium maturum ignotum stramineum superne sub(?)spinulosum; rostrum breve, pappus albus.

E sectione Alpinorum Haglund.

Typus: Gailtaler Alp.: Laserztörl, Lienzer Unholden, 14.8.1922 Vetter (W. 1950/1867); also in the neighbourhood: Kerschbaumer Törl, 1922 Vetter (W).

Furthermore:

Alp. de Savoie: Col de Salvadon 2200 m, 1898; Dent du Midi 25–2700 m, 1918; Val d'Illiez 2500 m, 1905; Grenairon — Col du Genivrier, 1898, all Briquet (G).

Mont Blanc: Buet, Col de l'Echaud, 1886 Jaccard (LAU).

Walliser Alp.: Col de Torrens 28–2900 m, 1919 Gandoger (RUEB).

Berner Alp.: Grand Muveran 28–2900 m, 1879 Burdet (LAU); Vallée de l'Etivaz, Thoumaley 2000 m, 1942 Maillefer (LAU); Dent de Morcles, 1907 Wilczek (LAU); Vallée de l'Avançon d'Anzeindaz, on several spots; Lagriaz 2060 m, Tête de Filasses 2130 m and 2145 m, Tortay 2300 m and 2340 m, all 1942 and 1943 Villaret (LAU); La Vire-aux-Boeufs 2350 m, 1947 Villaret (LAU); Gemmi, 1882 Chenevard (G); Lavaraz sur Bex, Thomas (W).

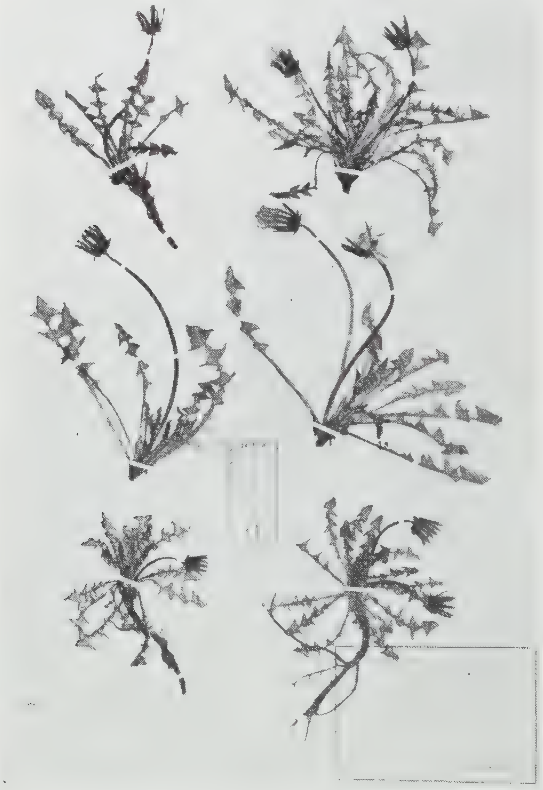

Fig. 10. T. vetteri v.S., type specimen.

Tessiner Alp.: Mt. Arera 2500 m, 1911 Chenevard (G); Passo Corombe 2460 m, 1951 Furrer (RUEB).

Glarner Alp.: Calanda 2150 m and 2550 m, 1941 and 1943 Büel (ZT).

Rhaetische Alp.: Piz Padella 2300 m, 1910 Branger (Z); Avers, Gletscherhorn 27–2800 m, 1895 v. Tavel (ZT); Albula pass 21–2300 m, 1948 v.S. (h); Val Tavrü towards Val Foraz, 1918 Schröter (ZT); Calanda 2700 m, 1917 Braun-Blanquet & Schröter, exsicc. Fl. Rhaet. 97 (G, LAU, RUEB, Z, ZT); Kupferfluh near Davos 2500 m, 1900 and Schiahorn 24–5002 m, 1910 both Schibler (Z); Mindersscharte near Pfunds, 1931 H.M. (W).

Bernina: Piz Languard 3000 m, 1953 Duvigneaud (h); Genistobel, Salzfluh 2600 m; Val Agoni (verisim.) and Piz Alv 27 2800 m, all Schröter (ZT).
Arlberg: 1908 Schneider (W).
Lechtaler Alp.: Valluga 1500 m, 1955 Melzer (h).
Amadello Gruppe: Campiglii, Valle Rendena 2560 m, 1874 Churchill (K).
Brenner: Wolfendorn, 1912 Vetter (W).
Zillertaler Alp.: Rohrbach, St. Johann 2000–2400 m, Treffer (W).
Salzburger Kalkalp.: Porsäule, Hochkönig, 1915 Vetter (W).
Hohe Tauern: Gamsgrube, 1904 Vetter (W); Gauskarl, Leitertal, 1937 Franz (W).
Gailtaler Alp.: Hochstadel, 1929 Schneider (W).
Totes Geb.: Hinterstoder, Priel, 1884 Kerner (GZU); Grosser Priel 1900 m and 2000–2100 m, 1923 Baumgartner (W).
Julische Alp.: Rogica near Kriz 2300 m, 1893 Dolenz (GZU).

This species is characterized by its yellowish stigmas and, especially, by its conspicuous dark involucres; pollen is absent; the lobes of the leaves are short, broad and dentate. It is very characteristic in the East Alps, but towards the West the sharp characteristics seem to fade away; some times the involucres are less dark, the outer involucral bracts some times narrower and more or less spreading; often pollen is present there, though mostly (or always?) sterile; the lobes of the leaves are less crispate and a little bit more hairy.

Most of the material that I have seen lack ripe achenes; this makes it difficult to decide if all these fluctuations really refer to *T. vetteri*. In western Switzerland the whole question becomes still more difficult, because also *T. carinthiacum*—so characteristic in the eastern Alps—there occurs in smaller forms, resembling to *T. vetteri*. In this region a further study is needed in which especially achenes are necessary.

Sectio Fontana van Soest

Plantae sat magnae et robustae raro graciles. Folia elongata integra vel sublobata vel interdum conspicue lobata; lobi laterales saepe retroversi; petiolis saepe late vel latissime alatis, purpureis vel saepe pallidis. Involucra viridia interdum glaucescentia; squamae exteriores vulgo adpressae, ovatae vel ovato-lanceolatae, saepe late marginatae, omnes laeves. Ligulae croceae vel saturate luteae. Floret aestate. Achenia straminea vel pallide brunnea, 3,5–5 mm longa (pyramide subbreve inclusa); rostra ca. 8 mm longa, pappus albus.

On humid and marshy spots and near wells in the upper subalpine and in the alpine region of high mountains: (1600–)1800–2400 m in Europe; from Corse through the Alpine chain into the mountains of south-eastern Europe.

The characteristic species of the section show nearly entire leaves with alate petioles, appressed, ovate and marginated outer involucral bracts and a long rostrum. *T. fontanum* H.M., in its broad sense, is more or less identical to the whole section; in its restricted sense, as used below, it represents the typical species for the section.

Some species show a remarkable resemblance to species of northern Europe, belonging to the sections *Spectabilia* Dahlst. and *Boreigena* Dahlst. The *Spectabilia*, however, are perfectly characterized by large achenes; the *Boreigena*, closely allied to the *Vulgaria* Dahlst., may have only a superficial resemblance to the *Fontana*.

KEY TO THE SPECIES OF SECT. FONTANA

1. Stigmas pure yellow 2
   Stigmas dirty yellow, greenish or blackish 4
2. Leaves grass-green with reddish petioles; pollen absent . . . . 9. *T. silvicolum*
   Leaves yellow- or grass-green with green, pale or brownish petioles; pollen present or not 3
3. Leaves grass-green; outer bracts of the involucre ovate, dark, appressed or erect; pollen absent . 8. *T. pseudoboreigenum*
   Leaves yellow-green; outer bracts of the involucre more or less lanceolate; pollen present . . . . . 11. *T. crocellum*
   Remark: compare also *T. pseudofontanum* in sect. *Alpina.*
4. Petioles of the leaves purple, seldom palish; outer bracts of the involucre with indistinct broad margine or only in *T. corsicum* with narrow margine. 5
   Petioles pale or brownish, median nerve sometimes brownish; outer bracts of the involucre ovate to lanceolate, without or with narrow but distinct margine 6
5. Pollen absent; outer bracts of the involucre with narrow but distinct margine . . . . 3. *T. corsicum*
   Pollen present; outer bracts of the involucre with broad but indistinct margine . . . . 1. *T. fontanum*
6. Marginal flowers lacking stripes or with weak and partly indistinct stripes, or with clear purple stripes 7
   Marginal flowers with distinct grey-violet stripes 9
7. Flowers nearly orange-coloured, without or with indistinct or purple stripes; leaves lobate, lobes 1,5–2 cm long; young leaves ± hairy . . . . 2. *T. aurantellum*
   Flowers dark yellow, without or with weak greyish stripes; young leaves nearly glabrous 8
8. Leaves entire or to coarse dentate; dents to 7 mm long . . . . 6. *T. peralatum*
   Leaves lobate, lobes 1–2 cm long . 5. *T. fontanosquameum*
9. Leaves to coarse and long dentate with broad middle field . . . . 4. *T. fontanicolum*
   Leaves distinctly lobate 10
10. Outer bracts of the involucre more or less appressed; petioles and median nerves pale . . . . 10. *T. aestivum*
    Outer bracts of the involucre distinctly recurved to reflexed; petioles and median nerves brownish, in dried condition to purplish brown . . . . 7. *T. pohlii*

1. **Taraxacum fontanum** von Handel-Mazzetti 1907. Monogr. Taraxacum: 100, c. icon.; emend. v. Soest.

The description, given by H.M., is broader and looser than it seems useful for a homogeneous species within *Taraxacum;* as far as

I know, no type specimen has been indicated by him; I will use the name "fontanum" with limitations in leaf form and completing the description with a few other data:

Folia lingulata denticulata vel anguste unguiculato-et retroverso-dentata, raro sublobata; lobi laterales angusti acuti; petiolis subalatis purpureis interdum subpallidis.

Scapus sub involucro glabrus vel parce araneoso-pilosus; squamae involucris exteriores ± adpressae ovatae, late inconspicue pallide marginatae; ligulae marginales extus parce vel e-striatae; antherae polliniferae; stylus et stigmata virescenti-lutea.

T. silvicolum m, likewise with purple petioles, has pure yellow stigmas. *T. corsicum* as well as *T. silvicolum* lack pollen and the leaves have a different shape. All the other species of this section have pale, whitish or brownish petioles; often the outer involucral bracts of these species are narrower and have no margine or only a narrow (but often distinct) one.

T. fontanum is indigeneous in the central and eastern Alps; H. M. has mentioned *T. fontanum* (sens. lat.!) from the Apennines, the Balcan Peninsula, the Caucasus and the Near East, regions, which I believe do not belong to the area of *T. fontanum* sens. str., even partly not to that of the section.

2. **Taraxacum aurantellum** van Soest **nov. spec.,** Fig. 11.

Planta robusta ad 20 cm alta.

Folia suberecta gramineo-viridia, juniores subdense araneoso-pilosa denique glabrescens, nervo mediano pallido vel roseolo-colorato, petiolis subnullis vel late alatis pallide viridis vel ± roseolis; folia 3–4 cm lata, lingulata ad 20 cm longa, acute et anguste retroverso- vel recurvo- vel patento-dentata, interiora saepe pro parte vel omnia lobata; lobi laterales utrinque ca. 3, triangulares saepe valde retroversi dorso saepe dentato, in interlobiis (ad 2 cm) latis dentatis abeuntes; lobus terminalis hastato-sagittatus acutus, interdum grosse dentatus vel sublobatus.

Scapi sub involucro subaraneosi.

Involucrum crassiusculum ca. 16 mm longum, ad 2 cm latum, obscure viride. Squamae exteriores laxe adpressae—erecto-patentes, apice recurvatae (denique reflexae) ovatae vel ovato-lanceolatae superne acuminatae summo obtuso purpureo, anguste marginatae apice minute ciliolatae; squamae interiores late lineares, inferne ad 5 mm latae, late membranaceo-marginatae, apice purpurascentes.

Calathium subradians ad 3 cm diametro, croceum; ligulae marginales angustae extus stria rubro-purpurea vel cano-purpurea ± notatae, apice obscurae; antherae parce polliniferae; stylus et stigmata virescenti-lutea; floret aestate.

Achenium rufo- vel obscure stramineum 4 mm longum pyramide inclusa) superne acute spinulosum ceterum rugosum—basi sublaeve, in pyramiden conicam 0,3 mm longam abrupte abiens; rostrum ca. 8 mm longum; pappus albus, 6 mm longus.

E sectione Fontanorum v. Soest.

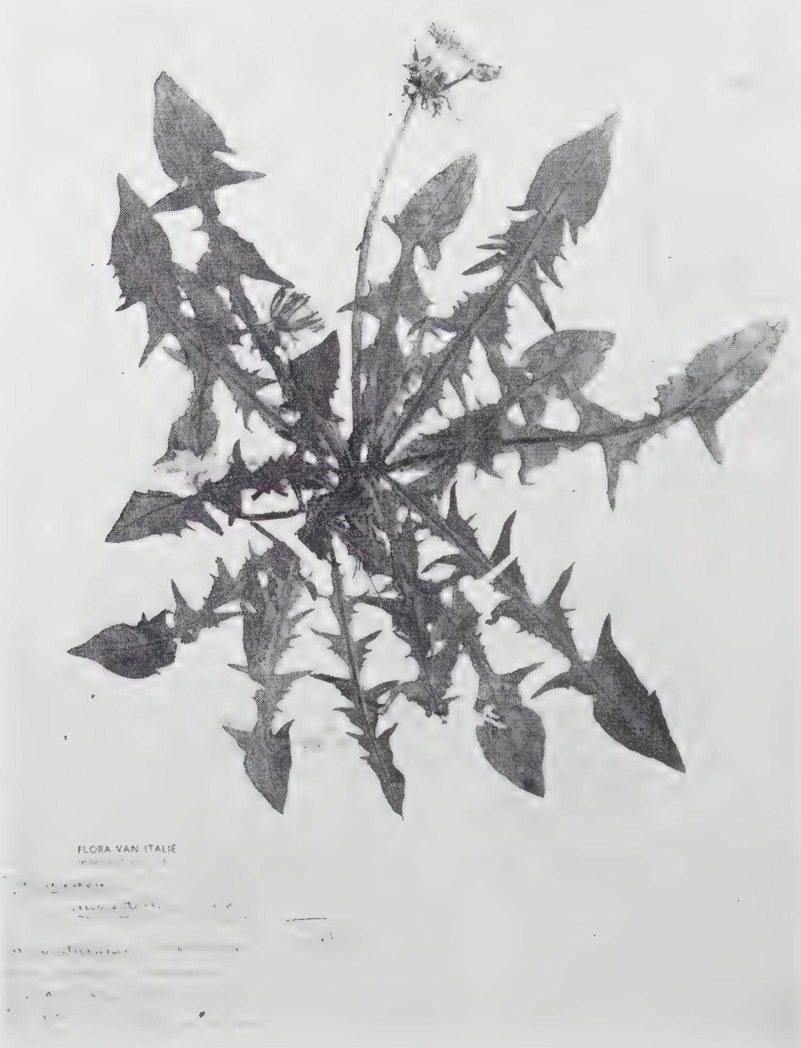

Fig. 11. T. aurantellum v.S., type specimen.

Typus: Oetztaler Alp.: Matschertal 1600–1650 m, 9.7.1956 v. Soest (h 36693–4, 36697, 36702, 36705, 36712, 36722–4).

Furthermore:

Hohe Tauern: Mallnitzer Tauerntal 1800 m, below Ebeneck, 1957 v.S. (h).

This species seems to be closely allied to *T. fontanosquameum* m, the latter having, in stead of orange-coloured, saturated yellow flowers and much shorter endlobes of the leaves.

f. stylosa v. Soest *f. nov.*: Ligulae marginales breves, stylosae: Oetztaler Alp.: Matschertal, 9.7.1956 v. Soest (h. 36866).

3. **Taraxacum corsicum** van Soest **nov. spec.,** Fig. 12.

Planta robusta ca. 20 cm alta.

Folia numerosa ad 10 cm longa terrae adpressa, laete gramineo-viridia subglabra, nervo mediano pallido, petiolis ± roseolis alatis vel pro parte anguste vel sub-alatis; folia exteriora obovata ± acute patento-vel retroverso-dentata, interiora incisa vel lobata; lobi laterales utrinque ad 3, triangulares subbreves, dorso interdum dentatis, margine inferiore integro, interlobiis inconspicuis vel latis; lobus terminalis magnus indeterminatus obtusus, subincisus vel ± deltoideo-dentatus vel integer; lobuli basis breves acuti.

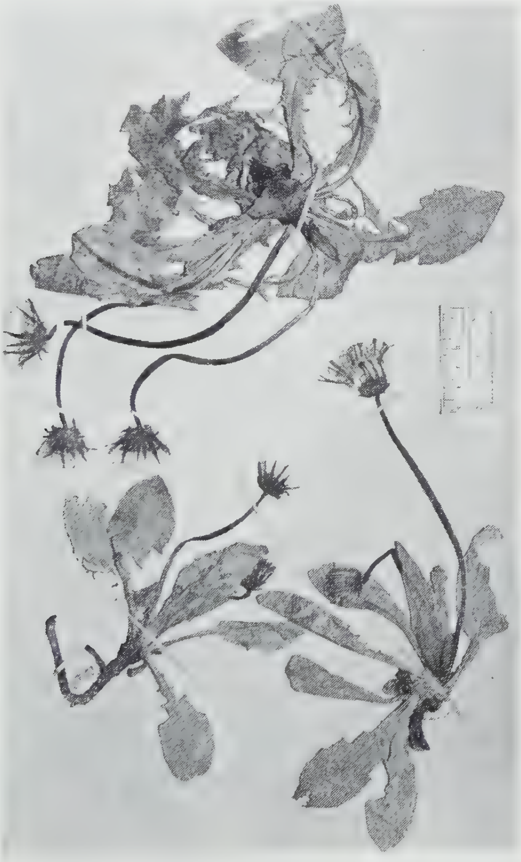

Fig. 12. T. corsicum v.S., type specimen.

Scapi ad 3, foliis subaequilongi vel eis superantes, sub involucro paulo araneosi.

Involucrum crassiusculum 16 mm longum, 14 mm latum, obscure viride. Squamae exteriores laxe adpressae ovatae ad 4 mm latae, ad 10 mm longae, ± acuminatae, anguste albo- vel roseolo-marginatae, laeves; squamae interiores late lineares membranaceo-marginatae.

Calathium planum radians ad 4 cm diametro, luteum; ligulae marginales planae, extus stria cano-violacea notatae, summis subnigrae; antherae vacuae; stylus sordide luteus; stigmata obscura siccis nigra; floret aestate.

Achenium 5 mm longum (pyramide inclusa), ochraceum, superne spinulosum ceterum rugosum—basi laeve, in pyramiden conicam 0,8 mm longam subsensim abiens; rostrum 7 mm longum; pappus albus, 5 mm longus.

E sectione Fontanorum v. Soest.

Typus: Corsica: Monte Niello, couloirs a l'Ubac, silice 2000 m, 16.7.1913 Wilczek (LAU); furthermore on the same mountain: Bergeries de Porciolelli 1950 m, 1913 Wilczek (LAU).

4. **Taraxacum fontanicolum** van Soest **nov. spec.,** Fig. 13.

Planta mediocris 5–16 cm alta, glabra vel parcissime araneosa.

Folia subdecumbentia luteo-viridia, exteriora lanceolata dentata, interiora et media lanceolata pro max. parte acute ± retroverso-dentata vel denticulata vel inconspicue lobata, lobis subintegris acutis summo retroverso, petiolis anguste vel saepe sublate alatis ± viridis vel nervoque mediano praesertim parte inferiore ± rufo-colorato.

Scapi 1–2, foliis breviter superantes vel aequilongi.

Involucrum 17 mm longum ovatum obscurum glaucescens. Squamae exteriores laxe patentes, apice recurvatae, lanceolatae vel ovato-lanceolatae 7–8 mm longae, 2–2,5 mm latae, inconspicue vel immarginatae, interiores lineares.

Calathium saturate luteum ad 3 cm diametro, radians; ligulae marginales extus stria ± atro-violacea ornatae; antherae polliniferae vel polline carentes; stylus et stigmata virescentia; floret aestate.

Achenium (speciminis non typici!) brunneum 3,7 mm longum (pyramide inclusa) ad 0,8 latum superne spinulosum ceterum rugosum, in pyramiden conicam 0,4 mm longam spinulis saepe praeditam subsensim abiens; rostrum 7 mm longum; pappus albus 5 mm longus.

E sectione Fontanorum v. Soest.

Typus: Rhaetische Alp.: Albula, Palpuogna, locus paludosus 1900 m, 31.7.1948 v. Soest (h. 19172, 19178, 19180–1, 19185, 19190). In the neighbourhood: Albula pass 21–2300 m, Val Mulix near Naz 1780 m, Val Tisch near Bergün above the Alp 1850–2100 m, all 1948 v. S. (h).

Furthermore:

Bernina: pass 2050–2250 m, 1948 v.S. (h); Lago Nero 2220 m, 1905 Braun & Rübel (RUEB).

Rhaetische Alp.: Corviglia 2400 m, 1957 Melzer (h); Buffalora-Ofenberg, 1901 Brunies (Z); Val Cluoza, 1909 Schröter (ZT).

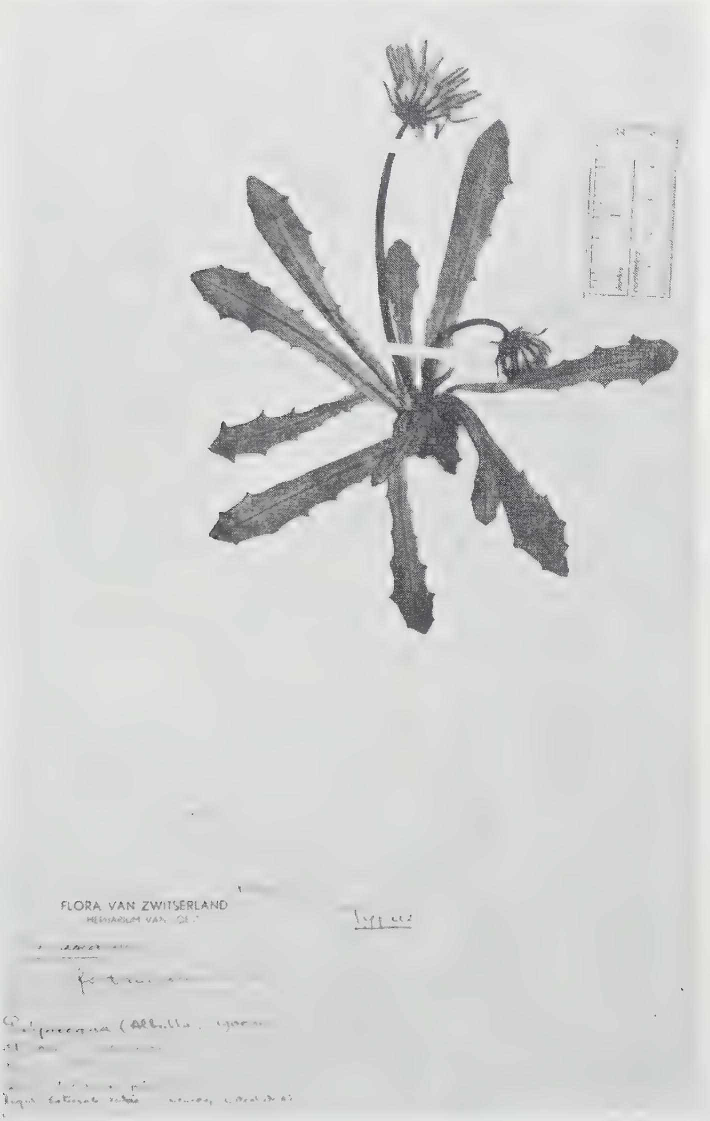

Fig. 13. T. fontanicolum v.S., type specimen.

Vorarlberg: Rautz 1650 m, 1903 Preissmann (W).
Ortler: Martelltal 21–2300 m, 1956 v.S. (h).
Brenner: Vennatal, 1926 Vetter (W).
Hohe Tauern: Prägraten, 1923 Vetter (W); Geiselkopf 1900 m and Hochalmblick near Mallnitz 2000 m, 1957 v.S. (h); Katschtal, Stern 2300 m and Franz Josefshöhe, Pasterze, 1934 Widder (h).
Dolomiten: Passo di Pordoi 2200 m, 1955 Keuchenius (U).
Karnische Alp.: Leitental 16–1800 m, 1955 Schaeftlein (h).
Tatra: Gr. Kohlbachtal, 1917 Schneider (W).

T. fontanicolum differs from *T. fontanum* s. str. by its broader-winged and pale petioles and, especially, by its recurved, narrower and often dark outer involucral bracts. *T. fontanicolum* has distinct dark stripes on the outside of the marginal flowers, as opposed to *T. peralatum* m, the latter having generally still broader wings of the petioles. *T. fontanicolum* has a slight resemblance to *T. helveticum* m (sect. *Alpina*); they differ in the character of the achenes and the outer involucral bracts; the achenes of *T. fontanicolum* are more spinulate and their beak is indistinctly delimitated, as contrasted with *T. helveticum*. *T. fontanicolum* has longer outer involucral bracts: 7–8 mm in stead of 5 mm; those of *T. helveticum* are acuminate with an obtuse apex; *T. helveticum*, smaller in size, has darker coloured styles and stigmas and darker, not greyish coloured involucres.

5. **Taraxacum fontanosquameum** van Soest **nov. spec.,** Fig. 14.

Planta robusta ca. 10–25 cm alta, subglabra.

Folia numerosa decumbentia laete viridia subtus pilis solitariis obsita, lanceolata vel oblanceolata valde grosse dentata vel lobata; lobi laterales utrinque ca. 3, pro max. parte triangulares acuminati summo retroverso, inferiores lanceolati peracuti vel, in foliis interioribus, triangulares dorso dentato; lobus terminalis deltoideo-sagittatus saepe grosse dentatus subobtusus ± plicatus; petiolis late alatis viridis.

Scapi crassi foliis subaequilongi vel eis superantes, glabri.

Involucrum 15 mm longum crassiusculum basi ovatum; squamae exteriores adpressae vel laxe patentes ca. 9 mm longae, 4 mm latae ovatae acuminatae conspicue albido-marginatae, interiores late lineares.

Calathium ± croceum 2,5–3 cm diametro, paulo radians. Ligulae marginales extus stria pallide violacea notatae vel saepe estriatae; antherae interdum polline carentes; stylus et stigmata virescenti-lutea. Floret aestate.

Achenium stramineum ca. 1,2 mm latum, 4 mm longum (pyramide inclusa), superne spinulosum ceterum rugosum—basi laeve, in pyramiden 0,6 mm longam late conicam apice pallidam sensim abiens; rostrum 9 mm longum; pappus albus, 6 mm longus.

E sectione Fontanorum v. Soest.

Typus: Bernina, pass 2050–2250 m, 18.7.1948 v. Soest (h. 19359).

Furthermore:

Rhaetische Alp.: Albula, Palpuogna 1900 m, Albula pass 21–2300 m and Weissenstein 2000–2100 m, all 1948 v.S. (h); St. Antonien, Partnun 2000 m, 1893 Schröter (ZT); Gotschnagrat near Klosters 2300 m and Stutzbachtal near Laret 1800 m, both 1954 v.S. (h).

Silvretta: Vernelatal 2000 m, Fremdvereina 1950 m, Seetal 2000–2050 m, all 1954 v.S. (h); Vermunttal, 1912 Vetter (W).

Hohe Tauern: Mallnitzer Tauerntal 1800 m, 1957 v.S. (h).

This species is allied to *T. peralatum* m, differing from it especially

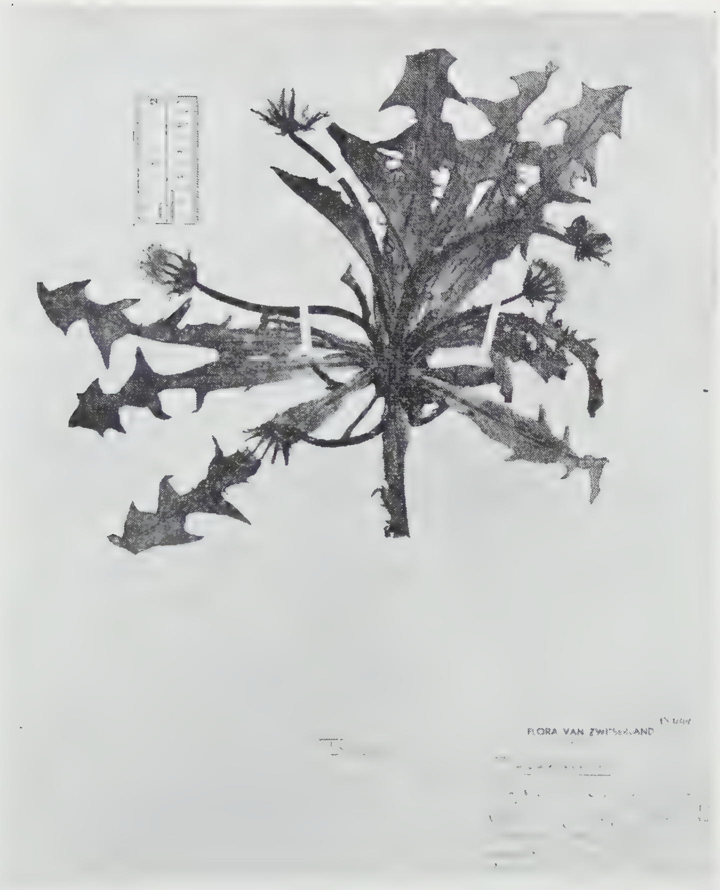

Fig. 14. T. fontanosquameum v.S., type specimen.

by its leaf form. Together with *T. peralatum* and *T. aurantellum*, it is characterized by the absence (or nearby absence) of stripes at the outside of the marginal flowers. Whilst *T. aurantellum* is more or less purplish-pink coloured here, giving, together with the dark yellow of the flowers, an impression of orange colour to the flowerheads, the flowers of *T. fontanosquameum* are only more or less saturated yellow. The leaves of *T. aurantellum* often are more divided, the endlobes are longer and, in the youth, they are more hairy.

6. **Taraxacum peralatum** van Soest **nov. spec.,** Fig. 15.

Planta mediocris 12–25 cm alta, ± epilosa.

Folia 10–20 cm longa gramineo-viridia, exteriora oblanceolata vel obovata ad 3 cm lata obtusa vel subacuta integra vel denticulata, petiolis subnullis; folia media et interiora oblanceolata ad 4 cm lata obtusa vel subacuta retroverso-dentata, saepius etiam denticulata vel

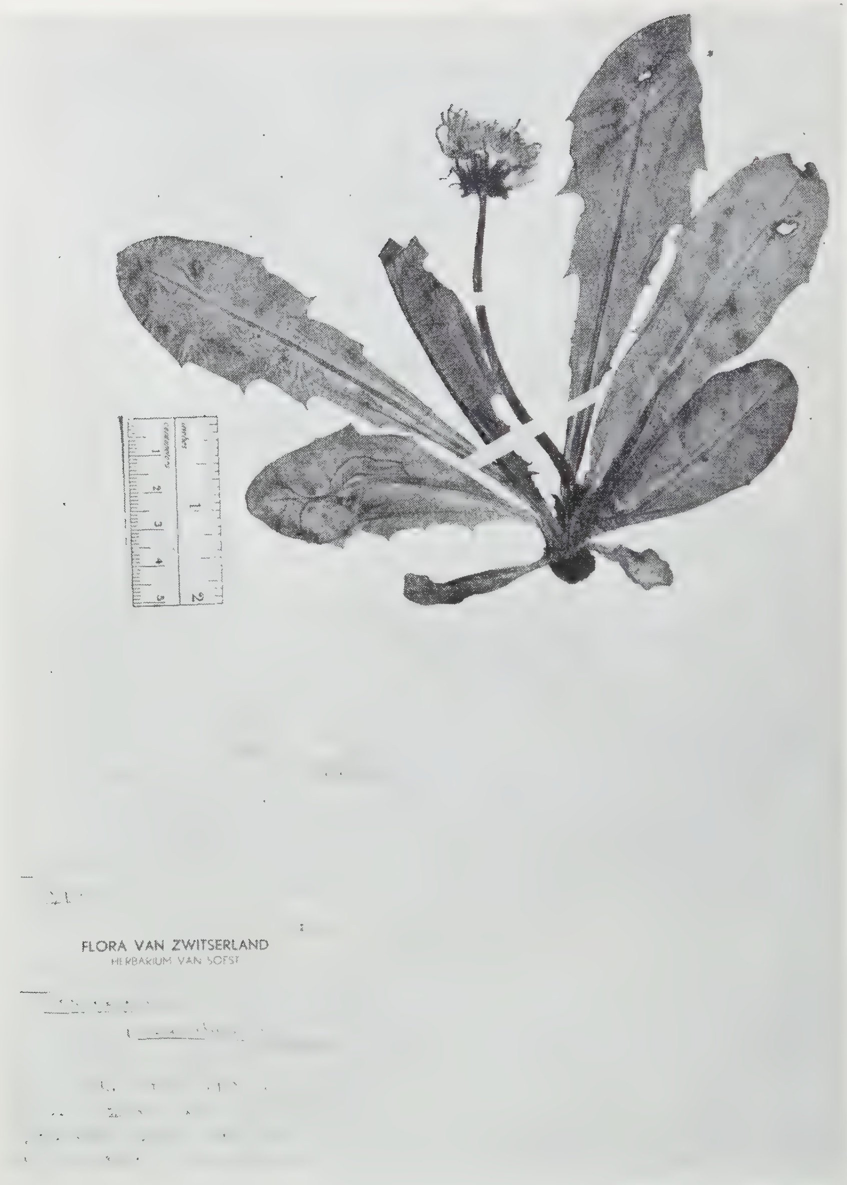

Fig. 15. T. peralatum v.S., type specimen.

raro sublobata, lobi laterales reflexae vel unguiculatae ad 10 cm longi, interlobiis latis (15 mm), nervo mediano pallido vel rufescenti.

Scapi 1–2, foliis aequilongi vel eis breviter superantes, sub involucro araneosi vel glabri, superne bracteolis praedito.

Involucrum 13–15 mm longum ovatum, obscure viride vel interdum purpurascente; squamae exteriores ± adpressae vel patentes apice recurvatae, ovatae longe acuminatae, conspicue anguste albido- vel purpureo-marginatae, interiores ad medium attingentes, extremae pro parte lanceolatae; squamae interiores lineari-lanceolatae.

Calathium paulo radians 2,5–3 cm diametro; ligulae marginales extus stria parce colorata notatae vel estriatae; antherae polline carentes vel repletae; stylus et stigmata obscura; floret aestate.

Achenium (speciminis non typici!) brunneo-stramineum subcylindricum 5 mm longum (pyramide inclusa) ad 0,8 mm latum, superne breviter spinulosum ceterum sublaeve, in pyramiden conicocylindricam 1 mm longam abrupte abiens. Rostrum 8 mm longum; pappus albus, 6 mm longus.

E sectione Fontanorum v. Soest, habitum speciorum sectionis Boreigeniae Dahlstedt imitans.

Typus: Rhaetische Alp.: Cuolm da Latsch, near Bergün 2100 m, 12.7.1948 J. C. van Soest (h. v. S. 19165).

Furthermore:

Rhaetische Alp.: Preda, Albula 1850 m and Palpuogna, in damp places, both 1948 v.S. (h).
Bernina: pass, 2050–2250 m, 1948 v.S. (h).

In the eastern Carpathians: Howerla Czorns Hora, 1888 Woloszczak (W), plants have been collected similar to *T. peralatum*, however with normal radiate flower heads and with yellowish green stigmas.

7. **Taraxacum pohlii** [1]) van Soest **nov. spec.,** Fig. 16.

Planta robusta 10–13 cm alta.

Folia gramineo-viridia ca. 10 cm longa, petiolo late alato inclusa, parce, sed in nervo mediano sordide rubescente densiuscule araneosa, sublobata vel lobata; lobi laterales utrinque 2–3, deltoidei vel triangulares breves acuti dorso interdum 1 dente muniti vel paulo denticulati, in interlobiis ca. 1 cm latis abeuntibus; lobus terminalis indeterminatus subdentatus subacutus.

Scapi saepe singuli, araneosi, sub involucro dense araneosi.

Involucrum 13 mm longum ad 2,5 cm latum crassum; squamae exteriores reflexo-patentes vel reflexae lanceolatae ad 10 mm longae pallide virides saepe purpurascentes laeves, interiores late lineares apice obscure virides.

Calathium planum radians ad 4 cm diametro, saturate luteum; ligulae marginales planae extus stria cano-violacea notatae; antherae polliniferae; stylus et stigmata subobscura. Floret aestate. Achenium maturum ignotum.

E sectione Fontanorum v. Soest.

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[1]) In remembrance of Dr. L. M. Pohl, Schlanders, excellent connoiseur of the Obervintschgau region; with greatest hospitality he guided and advised an excursion of the staff of the State Herbarium (Leiden) with students of the Leiden University to South Tirol (1956); a few days later he died during an alpine trip.

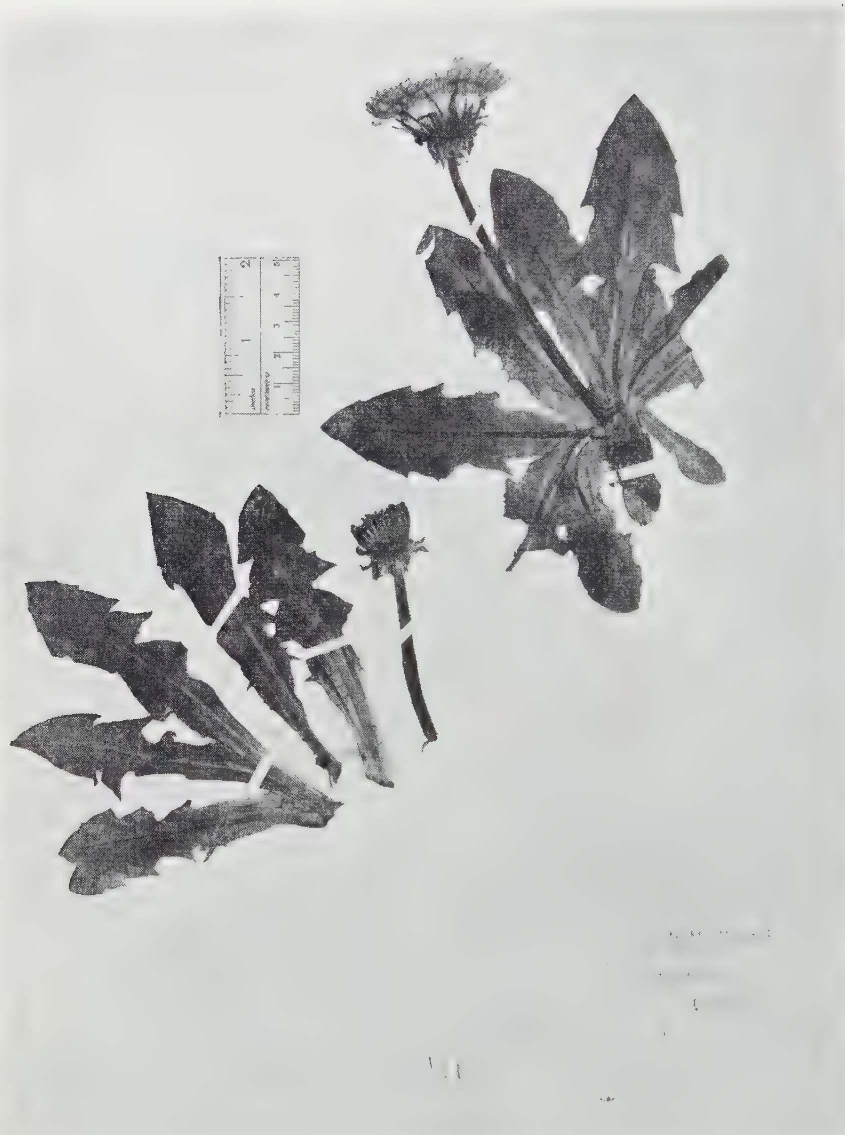

Fig. 16. T. pohlii v.S., type specimen.

Typus: Ortler: Martelltal 2350 m, 21.7.1956 v. Soest (h. 36804, 36884); in the same valley at 2300 m altitude, 1956 v. S. (h).

With regard to the flower heads this species is reminescent of the *Vulgaria* Dahlst.; other characteristics, such as the leaf form, show a close relationship to the *Fontana* m. The median nerve of the leaves is brown; after disappearance of the chlorophyll in some way or

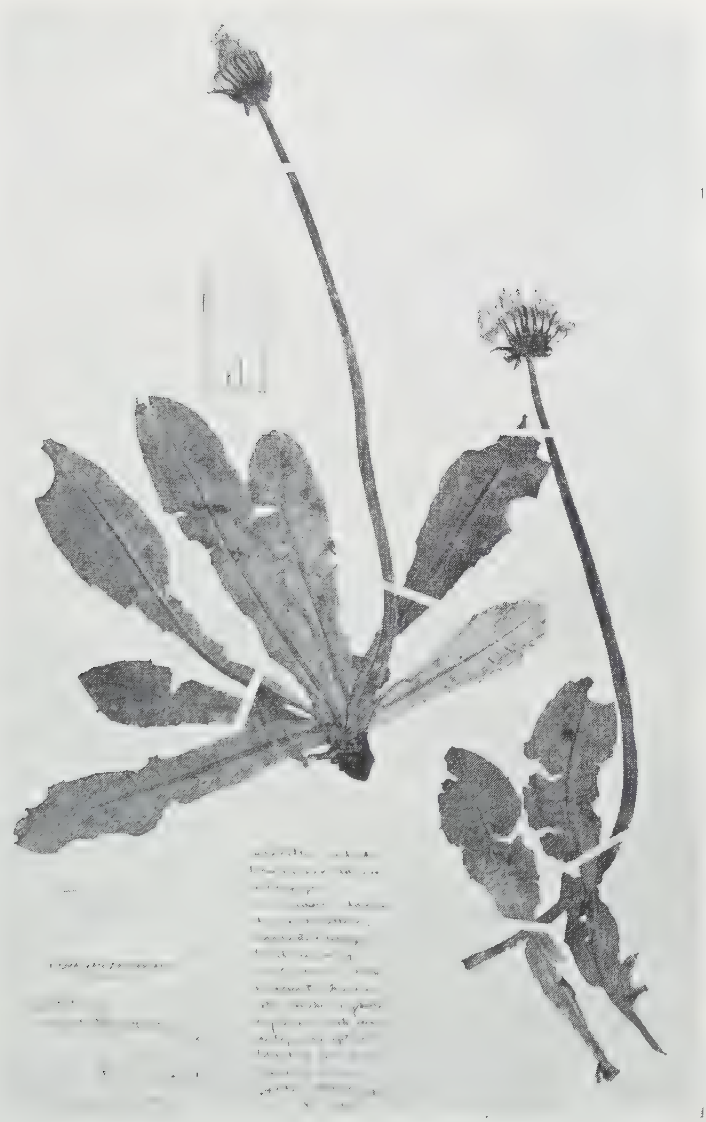

Fig. 17. T. pseudoboreigenum v.S., type specimen.

another, a deep purple is left. *T. pohlii* reminds one somewhat to northern species, belonging to sect. *Boreigena* Dahlst.

8. **Taraxacum pseudoboreigenum** van Soest **nov. spec.,** Fig. 17.

Planta magna robusta 40 cm alta, araneosa-hirsutula.

Folia luteo-viridia ad 20 cm longa ad 4 cm lata late lingulata integra minute retroverso-dentata vel saepe denticulata, subtus conspicue reticulato-venosa, nervo mediano lato araneoso basin versus rufo-purpureo, petiolis nullis vel latissime alatis.

Scapi crassi foliis superantes, sub involucro araneoso-pilosi.

Involucrum 20 mm longum crassiusculum basi ovatum subatratum; squamae exteriores ovatae 4 mm latae, 11 mm longae, anguste albo-marginatae erecto-patentes denique apice recurvatae.

Calathium obscure luteum radians, ad 4 cm diametro; ligulae marginales extus stria fusco-violacea ornatae; antherae polline carentes; stigmata et stylus aurea; floret aestate.

Achenium maturum ignotum, pappus albus.

E sectione Fontanorum v. Soest, habitum speciorum sectionis Boreigeniae Dahlstedt imitans.

Typus: Rhaetische Alp.: Albula, between Palpuogna and Preda, in silvis 1800–1900 m, 13.7.1948 v. Soest (h. 19168).

T. pseudoboreigenum is allied to *T. silvicolum* m, the latter being more slender and having purple petioles.

9. **Taraxacum silvicolum** van Soest **nov. spec.,** Fig. 18.

Planta robusta 13–18 cm alta, basi subglabra.

Folia erecta obscure viridia subaraneoso-pilosa, exteriora anguste spathulata saepe ± dentata, interiora oblanceolata retroverso-dentata vel lobata; lobi laterales utrinque ca. 2, triangulares acuminati dorso integro vel 1 dente munito; lobus terminalis ovatus subinteger obtusus vel subacutus vel subhastatus vel replete hastato-sagittatus; petiolis alatis nervoque mediano rubro-colorato.

Scapi erecti, foliis aequilongi, sub involucro dense araneosi, ceterum subaraneosi.

Involucrum 15–16 mm longum subobscure viride saepe purpurascens; squamae exteriores patentes apice recurvatae, 8 mm longae ovato-lanceolatae, acuminatae, late albo- vel roseolo-marginatae.

Calathium subradians ad 2,5 cm diametro; ligulae saturate luteae vel subcroceae, marginales extus stria fusco-violacea ornatae; antherae polline carentes; stylus et stigmata laete lutea; floret aestate.

Achenium olivaceo-stramineum ca. 6 mm longum (pyramide inclusa) ad 1 mm latum, superne acute spinulosum ceterum rugosum —basi laeve, in pyramiden conicam 0,8 mm longam subsensim abiens; rostrum 8 mm longum; pappus albus, 8 mm longus.

E sectione Fontanorum v. Soest.

Typus: Rhaetische Alp.: Val Tisch near Bergün 1800 m, 8.7.1948 v. Soest (h. 19164).

Furthermore:

Berner Alp.: Tour d'Anzeindaz, 1943 Villaret (LAU).

Rhaetische Alp.: Sagliaz. towards Val Tisch near Bergün 1800 m, Preda-Palpuogna, Albula and Albula pass 21–2300 m, all 1948 v.S. (h); Schlinigtal 1800 m, 1956 v.S. (h).

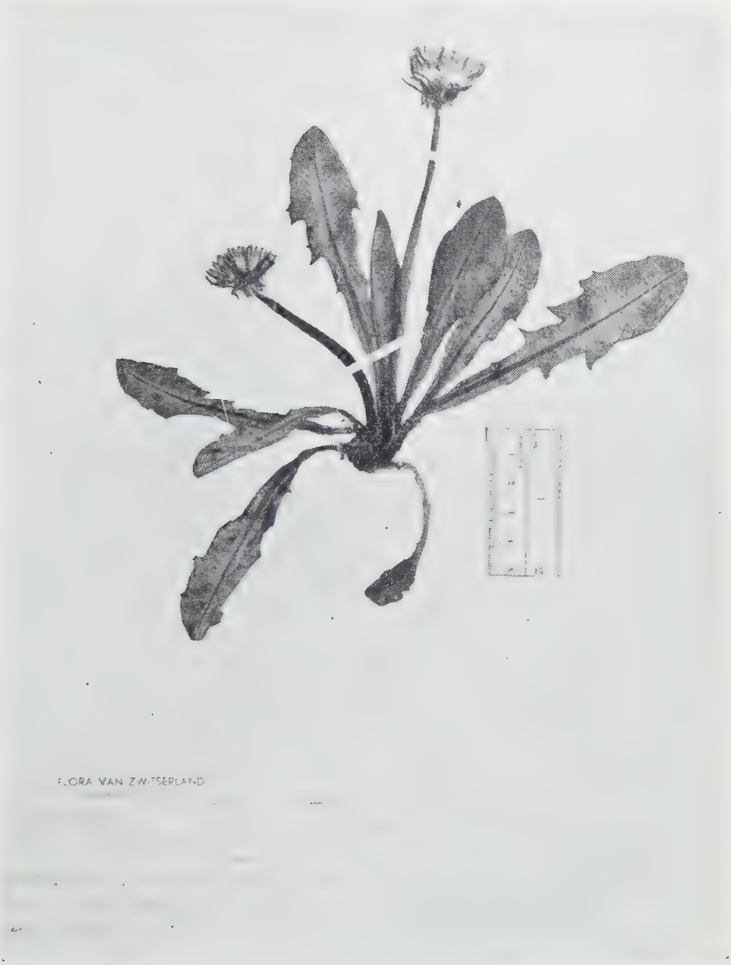

Fig. 18. T. silvicolum v.S., type specimen.

The purple petioles are an easy characteristic in order to distinguish this species from most others of sect. *Fontana*; the difference with *T. fontanum*, with the same characteristic, is mentioned above. *T. silvicolum*, furthermore, is characterized by pure yellow stigmas as in *T. pseudoboreigenum*, the latter having green or slightly brownish petioles.

10. **Taraxacum aestivum** van Soest **nov. spec.,** Fig. 19.

Planta gracilis ad 20 cm alta inferne glabra, basi fragmentis foliorum vetustorum subincrassata.

Folia numerosa luteo- vel gramineo-viridia, glabra, nervo mediano pallido petiolis subalatis pallide viridis. Folia exteriora lingulata

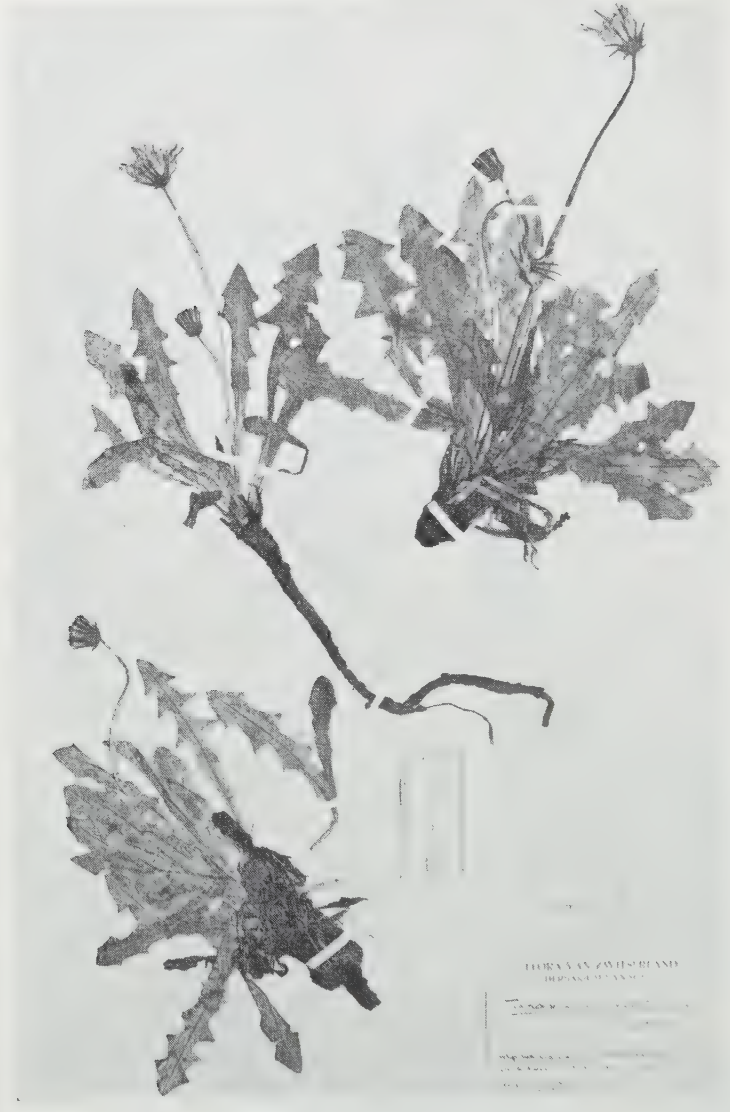

Fig. 19. T. aestivum v.S., type specimen.

saepe grosse dentata, interiora lobata; lobi laterales triangulares ca. 1 cm longi dorso denticulato, interlobiis ca. 7 mm latis denticulatis vel minute dentatis, lobus terminalis deltoideus vel hastatus vel hastato-sagittatus saepe integer, lobulo apicali subacuti vel subobtusi, lobuli basis acuti.

Scapi foliis aequilongi vel breviter superantes, sub involucro subaraneosi.

Involucrum mediocre 12 mm longum, 14 mm latum, viride pruinosum; squamae exteriores laxe adpressae vel subpatentes, ovato-lanceolatae immarginatae apice pallidae.

Calathium planum radians ad 2,5 cm diametro; ligulae luteae, marginales extus stria fusco-violacea notatae; antherae parce polliniferae; stylus et stigmata virescenti-lutea; floret aestate.

Achenium maturum ignotum, luteo-brunneum, superne minute(?) spinulosum; pappus albus.

Typus: Bernina: Alp Languard, in silvis 1950 m, 25.7.1933 v. Soest (h. 4603).

Furthermore:

Bernina: Piz Languard 2400 m, 1933; Chaputschöll, 1929 and Bernina pass 2050–2250 m, 1948, all v.S. (h); Lago Bianco, 1930 W. Koch (ZT).
Rhaetische Alp.: Albula, near Weissenstein 2050 m, 1948 v.S. (h); Dischmatal near Davos, 1899 Hegi (Z).
Stubaier Alp.: Gschnitztal, Alpe Lapones 18–1900 m, 1903 H.M. (W).
Ortler: Martelltal 21–2300 m, 1956 v.S. (h).

11. **Taraxacum crocellum** van Soest **nov. spec.,** Fig. 20.

Planta gracilis 10–20 cm alta glabra.

Folia luteo-viridia tenera lanceolata vel oblanceolata dentata vel lobata; lobi laterales utrinque ca. 2, breves saepe anguste deltoidei vel anguste triangulares summo retroverso acuti dorso interdum dentato, interlobiis latis; lobus terminalis indeterminatus vel hastato-sagittatus integer apice subobtusus vel subacutus; petiolis pallide viridis interdum paulo subalatis.

Scapi foliis superantes.

Involucrum mediocre 12 mm longum 12 mm latum, basi subtruncatum viride subpruinosum purpurascens; squamae exteriores laxe adpressae lanceolatae vel ovato-lanceolatae 7 mm longae ca. 2,5 mm latae, pallide inconspicue marginatae, interiores lineares membranaceo-marginatae.

Calathium planum radians ad 2,5 cm diametro ± croceum; ligulae marginales extus stria cano-violacea notatae; antherae polliniferae; stylus et stigmata laete lutea; floret aestate.

Achenium stramineum, maturum ignotum; pappus albus.

Typus: Silvretta: Vernelatal 2150 m, 18.7.1954 v. Soest (h. 33698, 33799, 33800, 33802).

Furthermore:

Silvretta: Vernelatal 2050 and 2250 m, Süsertal 2100 m, Vereinahaus 1950 m and Seetal 2000 m, all 1954 v.S. (h).
Oetztaler Alp.: Matschertal 1650 m, 1956 v.S. (h).

T. crocellum probably belongs to the *Fontana*; it seems closely allied to *T. aestivum* m, the latter having more yellow flowers, no pure yellow stigmas and a greyish involucre. *T. crocellum* is reminescent of the *Alpina*; as soon as ripe achenes are to my disposal I better shall be able to decide whether it belongs to *Fontana* or *Alpina*. There is

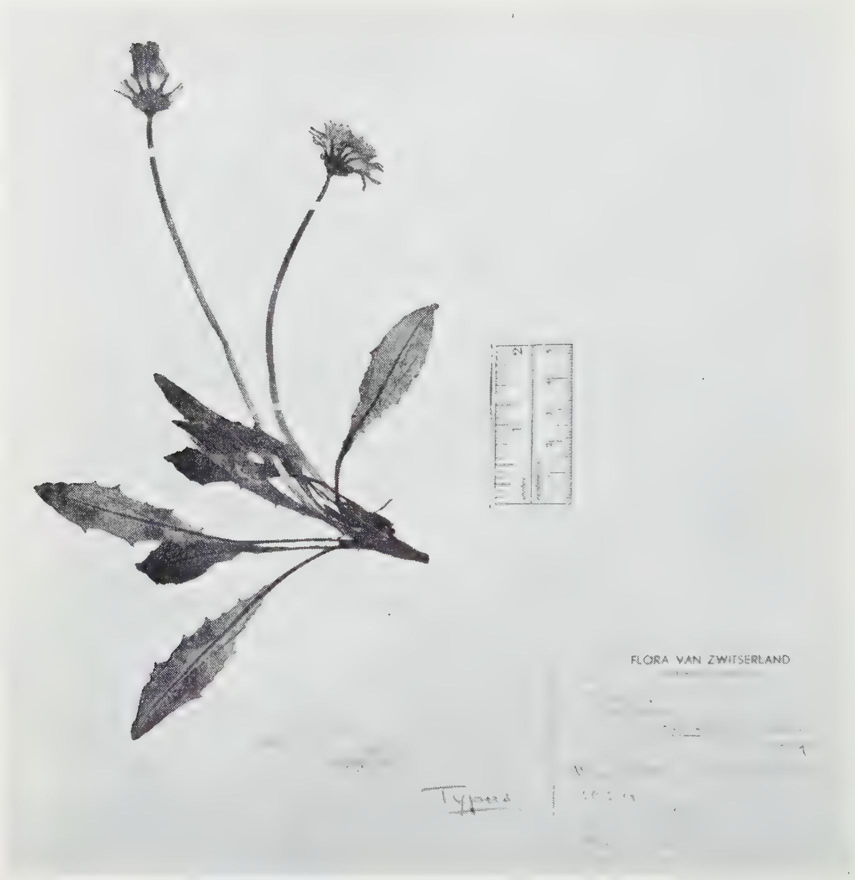

Fig. 20. T. crocellum v.S., type specimen.

some resemblance to *T. petiolulatum* Huter (sect. *Alpina*), but the involucres are different; furthermore, *T. crocellum* has more dentate leaves, a narrower apex of the leaves and pure yellow stigmas.

Sectio Cucullata van Soest

Plantae subglabrae vel paulo araneosae. Petioli foliarum pallidi vel leviter colorati. Involucra obscure virescentes, squamae exteriores ± adpressae, erecto-patentes vel ± recurvatae. Ligulae pallide ochraceo-luteae, marginales ± involutae, tubulosae vel stylosae, extus stria roseo-purpurea notatae vel ± decoloratae. Achenia olivacea ca. 4 mm longa (pyramide inclusa) superne tenuiter spinulosa, rostrum longum, ca. 7–8 mm; pappus albus.

Plants of the whole chain of the Alps at 1700–2400 m altitude, also in Corse.

This section is allied to both the *Alpina* Hagl. and the *Fontana* m; the involucres show relationship to the first section, the achenes to the second one. This section, however, is no intermediate group between both; the pale ochraceous colour and the peculiar form of the ligulas are remarkable. In the genus *Taraxacum* the colour of the flowers has a rather wide amplitude: white (for instance in *T. leucanthemum* Ledebour), pale yellow (for instance in sect. *Erythrosperma* Dahlst. em. Lb. f in majority), saturate yellow (sect. *Vulgaria* Dahlst. for instance) to orange-red or "croceus" (certain *Fontana*) or "aurantiacus (*T. aurantiacum* Dahlst.); even pink and purplish in central Asian forms (*T. roseum* H. M., *T. porpyranthum* Boissier). The ochraceous colour, nearly the colour of straw, is only characteristic in sect. *Cucullata*, of which *T. cucullatum* Dahlst. represents the type species.

1. **Taraxacum cucullatum** Dahlstedt 1907. Acta Horti Bergiani *4.2*: 25, c. icon.; *T. stramineum* Beauverd 1929. Bull. Soc. Bot. Genève: 138, pro parte?. I have seen the type specimen in h. S.: cultivated in Bergianske Trädgården, Stockholm, 3.8.1901 from achenes collected in Salzburg.

This species is not rare in the Alps. I refer to Bonnier 1930/1933, Flore de France: 6; Hegi 1928, Flora Mitt. Europa *6.2*: 1093; von Handel–Mazzetti 1923. Oesterr. Bot. Zt. *72*: 269; Becherer 1956. Ber. Schweiz. Bot. Ges. *66*: 192 and 1958. *68*: 238. Certainly it is not only a species of the western region, as suggested by Hegi; from the central and eastern region I have seen:

Churfirsten: Breitenalp — Selamatt 16–1700 m, 1914 Vogt (Z).
Vierwaldstädter Alp.: Gletsch 2000 m, 1920 Christ (ZT).
Rhaetische Alp.: Avers-Cresta 1960 m and Thäli, both 1938 v.S. (h); Val Tisch near Bergün 1850–2100 m, 1948 v.S. (h); Alp Casanna, Ober-Säss 2030 m, 1913 Noack (RUEB).
Oetztaler Alp.: Vent-Ramoljoch 2500 m, who? (AMD).
Sarntaler Alp.: Jauffen, 1910 Schneider (W).
Hohe Tauern: Waschgangalpe, Leiter, Radenalpe near Sagritz, 1851 Pacher, exsicc. Schultz Bip. Cichor., pro parte (W); Mallnitz, 1929 Schneider (W); Mallnitzer Tauerntal 1850 m, 1957 v.S. (h).
Niedere Tauern: Radstädter Tauern, 1897 Kann (GZU); Radeckalpe, Ankogl 1700 m, 1913 Fritsch (GZU); Lungau, Zaunersee 2050 m, 1926 H.M. (W).
Schneeberg (Nied. Oesterr.): Damböckhaus 1800 m, 1957 Melzer (h).

2. **Taraxacum tiroliense** Dahlstedt 1907, Acta Horti Bergiani *4.2*: 23, c. icon.; *T. alpinum* var. *ochroleuca-tubulosa* Hellweger in sched. 1891 and in Dörflers Katalog 1902: 180.

This species only is known from the eastern Alpine region: I saw:

Bernina: Piz Lagalb 2550 m, 1933 v.S. (h).
Rhaetische Alp.: Lünersee near Bludenz, 1911 Vetter (W).
Oetztaler Alp.: Vent, Neurautner (GZU); Tösens 2500 m, 1926 H.M. (W).
Sonnenwend Geb.: Sonnenwendjoch 2226 m, 1891 Hellweger (S, W), Hellweger's type material; also near Ienbach 2100 m, 1903 Hellweger (RUEB).
Zillertaler Alp.: Varnatal, 1926 Vetter (W); Weissenbach 2000–2400 m, 1890 and 1897 Treffer (GZU, LAU, O, S), mentioned by Dahlstedt; Luttach

2000–2400 m, 1897 and 1898 Treffer (G, GZU, LAU); the type specimen in h.S.! is a cultivated plant in Bergianske Trädgården, Stockholm 1906 Dahls., from achenes from Luttach; Voldertal 1850 and 2000–2100 m, H.M. (W).
Gailtaler Alp.: Laserzwand, 1928 Gáyer (GZU).
Deferegger Alp.: 26–2700 m, 1934 H.M. (W); Lienz, Kühbodental 1770 m, 1932 H.M. (W).
Hohe Tauern: Böseck, Tauerntal 1600 m, 1957 Viola v. Soest (h. v.S.).
Karnische Alp.: Obstansersee near Kartitsch 2330 m and Leitental, Fillmoor 16–1800 m, both Schaeftlein (h).

3. **Taraxacum fontaniforme** van Soest **nov. spec.,** Fig. 21.

Planta mediocris 12 cm alta, tota glabra.

Folia 6 cm longa (petiolis subnullis alatis inclusa) luteo-viridia lanceolata vel ovato-lanceolata acuta, retroverso-denticulata.

Involucrum viride, obscure punctatum. Squamae exteriores laxe patentes apice ± recurvatae, ovato-lanceolatae acuminatae ad 7 mm longae, late albido- vel purpureo-marginatae apice roseolae; squamae interiores late membranaceo-marginatae, 14 mm longae apice rubro-violaceae.

Calathium mediocre flavum; ligulae marginales pro max. parte involutae, extus vinoso-coloratae, apice obscure purpureae. Styli

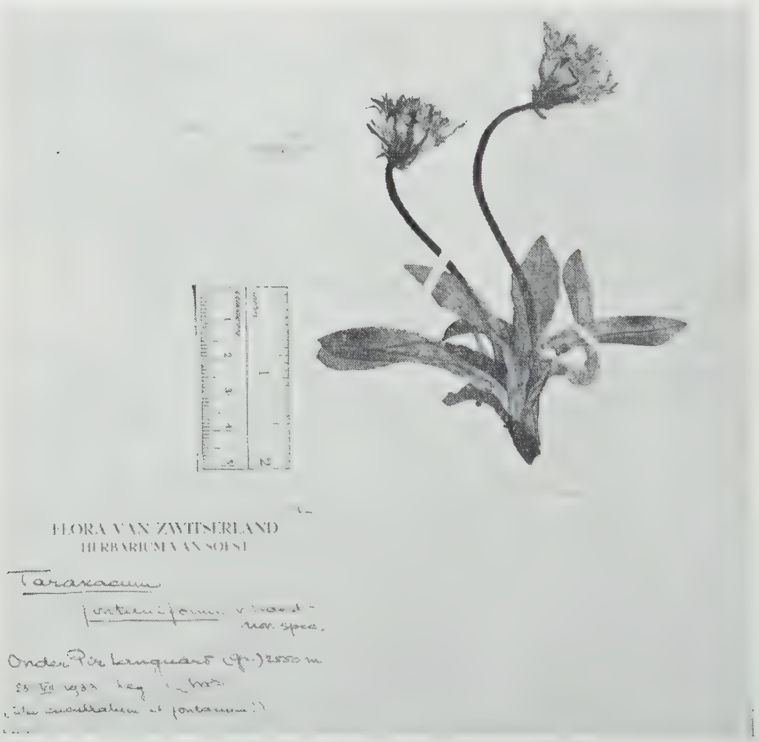

Fig. 21. T. fontaniforme v.S., type specimen.

inferne lutei, superne purpurei; stigmata obscure purpurea, siccis subnigra; antherae vacuae. Floret aestate. Achenium maturum ignotum.

E sectione Cucullatorum v. Soest.

Typus: Bernina: Piz Languard 2550 m, 25.7.1933 v. Soest (h. 4601).

The leaves of this species are reminiscent of those of *T. fontanum* H.M., but *T. fontaniforme* can be recognized by the pale yellow, not straw-coloured flowers. It has beautiful purple stigmas and even the upper part of the styles is light reddish purple; I never saw this colour of stigmas and styles elsewhere in this genus.

4. **Taraxacum cucullatiforme** v. Soest 1957. Acta Botan. Neerl. *6*: 417, c. icon.

This species, only known from Corse: Monte Renoso and Monte Rotundo, is also collected: Monte d'Oro 18–2100 m, herb. Salis-Mraschlins (ZT).

SECTIO RHODOCARPA VAN SOEST

1. **Taraxacum schroeterianum** v. Handel-Mazzetti 1905. Oesterr. Bot. Zt. *55*: 461; Monogr. Tarax. 1907: 104, c. icon.; Oest. Bot. Zt. 1922. *71*: 270; Braun–Blanquet & Rübel, Fl. Graubunden, 1936: 1417; v. Soest 1954. Collectanea Bot. *4.1*: 16; and 1954. Vegetatio *5/6*: 527.

T. rhodocarpum Dahlst. 1907, Acta Horti Bergiani *4.2*: 21.

T. officinale ssp. *Schroeterianum* Schinz & Keller, Fl. der Schweiz.

T. laevigatum ssp. *Schroeterianum* Hegi 1928. Fl. Mitteleur. *6.2*: 1094.

The area of this species is: Spain (Sierra de Guadarrama) and the alpine chain from the Alpes Maritimes to eastern Switzerland; *T. schroeterianum* is not known from the Pyrenees. Localities, not mentioned in the literature, are listed below.

Walliser Alp.: Grand St. Bernard 2450 m, 1921 Wilczek (LAU); Alpe Breuillet 2300 m, 1910 Wilczek (LAU); Mattmark, Saastal 2100–2350 m, 1937 Maillefer (LAU); Saas-Fée — Saas Almagell 1800 m, Almagelltal 21–2200 m, Distelalp 2150–2250 m, Tälliboden 23–2400 m, all 1952 v.S. (h); Col de la Gueula 1960 m, 1917 Moreillon (LAU).

Vierwaldstädter Alp.: Göschenen 1100 m, 1906 A. S. Peax (Gray herb.); Surenenpass 15–1800 m, 1866 Brügger (ZT).

Tessiner Alp.: Valle Mesocco, Valle Leggia, 1917 Guralser (RUEB).

Rhaetische Alp.: Albula pass 21 2300 m, Weissenstein 2050 m, Palpuogna 1900 m, all 1948 v.S. (h); Lampertschalp and Zervreila, Vals, Wüller (CHUR); Parsenn Hütte 2200 m, slope of Lauenenzughorn 1320 m, Schlappintal near Klosters 1650 m, Landquart valley below Alp Pardenn 1320 m, all 1954 v.S. (h).

Bernina: Hospiz 2300 m, pass 2050–2250 m, both v.S. (h); Flatz valley near Pontresina 1850 m, 1933 v.S. (h); south slope of Piz Lagalb, 1944 W. Koch (ZT).

Silvretta: Alp Sardasca 1640–1650 m, Alp Fremdvereina, Jörital 1950 m, both 1954 v.S. (h).

2. **Taraxacum rufocarpum** van Soest **nov. spec.**

Planta mediocris vel robusta, ca. 10–15 cm alta, subglabra (scapi sub involucro interdum et folia subtus paulo araneosi), basi fragmentis foliorum vetustorum subincrassata.

Folia numerosa suberecta ad 13 cm longa, ad 3 cm lata, gramineoviridia, lobata; lobi laterales utrinque ad 4, hamati vel deltoidei vel triangulares, subacuti ± crispati, dorso integro vel saepe magis dentato, margine inferiore saepe valde concavo integro, summo saepe retroverso, in interlobiis brevis vel subnullis ad 5 mm latis interdum magis dentatis ± abeuntibus; lobus terminalis hastatus vel ± deltoideus, ad 2 cm longus, ad 3 cm latus, vel interdum elongatus subobtusus, integer vel utrinque 1 dente grosso munitus, lobuli basis retroversi subacuti; petiolis alatis (5–10 mm latis) nervoque mediano pallido vel subrufescente. Folia exteriora saepe ± lingulata sublobata vel grosse dentata.

Scapi 1–3, floriferi foliis aequilongi vel eis breviter superantes.

Involucrum crassiusculum ca. 15(–18) mm longum, ad 14 mm latum, saepe obscure viride. Squamae exteriores apice recurvatae oblanceolatae ad 7 mm longae 3 mm latae obtusae parum roseoviolaceae, inconspicue marginatae, laeves; interiores apice violaceae, late membranaceo-marginatae, laeves.

Calathium 2,5–4 cm diametro, luteum. Ligulae marginales planae, extus stria purpurea notatae. Antherae saepe parce polliniferae; stylus luteus, stigmata fusco-lutea. Floret aestate.

Achenium 4 mm longum (pyramide inclusa) rufum vel aurantiacum, superne spinulosum (spinulis erectis) ceterum rugosum basi laeve, in pyramiden conicam ca. 0,5 mm longam spinulis interdum praeditam subsensim abiens. Rostrum 5 mm longum; pappus niveus, 4–5 mm longus.

Typus: Hohe Tauern: Hochalmblick below Schönbretterspitze 2000 m, 25.7.1957 v. Soest (h. 37978–80, 37982).

Furthermore:

Alp. Maritimes: 1887 Favrat (ZT); possibly: Mt. Mounier 2750 m, 1904 St. Yves (LAU).

Alp. de Savoie: Pointe de Finive 24–2500 m, 1917; Mt. Buet, Fer-à-Cheval 2300 m, 1904; Col de Barbérine 2400 m, 1904, all Briquet (G).

Walliser Alp.: Rappental 2300 m, 1915 Burnat & al. (LAU).

Berner Alp.: Col du Rawil, Iffigenalp, 1906 Wilczek (LAU).

Churfirsten: Käserruck 2150 m, 1941 W. Koch (ZT).

Rhaetische Alp.: Oberengadin, Laret 2080 m, 1930 W. Koch (ZT); Parsennhütte near Klosters 2200 m, 1954 and Schlinigtal 1800 m, 1956 v.S. (h).

Bernina: Forno, 1898 Schinz & Hegi (Z); Cacciabella pass, Bergell 2700 m, Rikli (ZT).

Stubaier Alp.: Magdalenertal, Muttenjoch 2700 m, 1872 Churchill (K).

Eisenerzer Alp.: Hochschwab 2000 m, 1953 Rechinger (W).

Hohe Tauern: Mallnitzer Tauerntal, below Geiselkopf 1900–2000 m, below Ebeneck and below Mallnitzer Tauern 1900 m, Dössenersee 2250-2300 m, Franz Josefshöhe 2420 m, all 1957 v.S. (h); Kals 1900 m, 1931 H.M. (W); Waschgangalpe, Pacher in Schultz Bip. exs. 74, pro min. parte (K).

Dolomiten: Durmalp, Fassatal *or* St. Pellegrino in Fiemme, Facchini, exs. Rchb. 1958 (L. W); the same exsicc. contains *T. panalpinum* m.; it is difficult to

decide which of both localities belongs to *T. rufocarpum*; both species extend their area as far as the western Balcans.

Hercegovina: Trinaue, Pleša pl., 1911 Schneider (W).

It is still uncertain to which section *T. rufocarpum* belongs. The rostrum is too short to consider it as one of the *Fontana*; the outer involucral bracts show little relation with those of species of the *Alpina*; in other characters *T. rufocarpum* shows affinity to the latter section. It differs from *T. schroeterianum* in colour of the achenes, the shape of the outer involucral bracts, the green, slightly winged petioles.

Sectio Vulgaria Dahlstedt

In the subalpine region a few species of sect. *Vulgaria* seem to be really native; some of these are described below. They constitute more or less a transition between the characteristic *Vulgaria* of the European plains and the *Fontana* and *Alpina*.

Though, from a morphological point of view, it is not easy to make a distinct difference between this subalpine group and the characteristic *Vulgaria*, their behaviour seems to be different. The last ones are mostly introduced in the higher regions along roads, even up to high altitude. Both groups do not bloom until June or July. The introduced forms, however, show an excessive or abnormal growth ("status aestivalis"); the native, subalpine forms behave completely normal. In cultivation (in my garden, Delft) the latter bloom nearly a month later than the *Vulgaria* of the European plains.

1. **Taraxacum aequilobiforme** van Soest **nov. spec.,** Fig. 22.

Planta sat robusta ca. 15 cm alta.

Folia numerosa multilobata luteo-viridia, parce, in nervo dorsali densiuscule araneosa, petiolis subalatis pallidis. Lobi laterales utrinque 5–8, falcati vel anguste triangulares acuti, dorso saepe valde convexo integro vel raro dentato, margine inferiore integer, angulis loborum plicatis; interlobiis longiusculis (ad 10 mm longis), ad 5 mm latis, saepe dentatis vel pergrosse dentatis; lobus terminalis sagittatus, lobuli basis acuti integri, lobulo apicali elongato subacuto.

Scapi foliis aequilongi vel eis breviter superantes, sub involucro densiuscule araneosi.

Involucrum ca. 15 mm longum, ca. 18 mm latum, basi rotundatum. Squamae exteriores ovatae vel ovato-lanceolatae ca. 10 mm longae obscure virides subglaucescentes, laxe adpressae apice recurvatae, subconspicue vel pro parte inconspicue marginatae, ciliolatae; squamae interiores late lineares membranaceo-marginatae.

Calathium paulo radians 2,5–3 cm diametro, obscure luteum. ligulae marginales angustae evittatae vel paulo roseolae. Antherae (saepe parce) polliniferae; stylus et stigmata laete lutea. Floret aestate (in regione alpina!).

Achenium stramineum 4 mm longum (pyramide inclusa) superne spinulosum ceterum rugosum—basi laeve, in pyramiden conico-

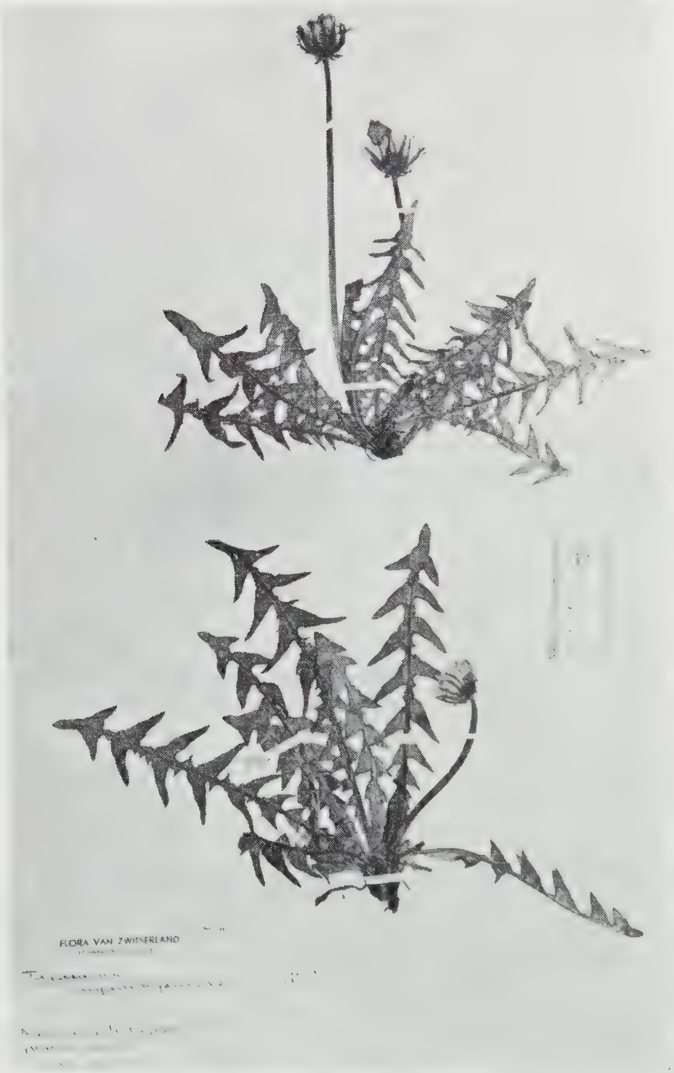

Fig. 22. T. aequilobiforme v.S., type specimen.

cylindricam ad 0,7 mm longam (spinulis saepe praeditam) abrupte abiens. Rostrum ca. 8 mm longum; pappus albus ca. 5 mm longus. E sectione Vulgariorum Dahlstedt.

Typus: Walliser Alp.: Saas-Fée, northwest slope of Mittaghorn 2000 m, 16.7.1952 v. Soest (h. 31113–8); furthermore in the same region: Kalbermatten 1900 m, Fée–kessel 18–2000 m and towards Almagelltal 1800 m, all 1952 v. S. (h).

2. **Taraxacum callosum** van Soest **nov. spec.,** Fig. 23.

Planta sat humilis 4–11 cm alta, basi fragmentis foliorum subincrassata.

Folia decumbentia gramineo-viridia ad 10 cm longa, parce araneosa; lobi laterales utrinque 3–4, triangulares retroversi vel ± deltoidei vel saepe breve et late unguiculati subacuti, dorso denticulato vel

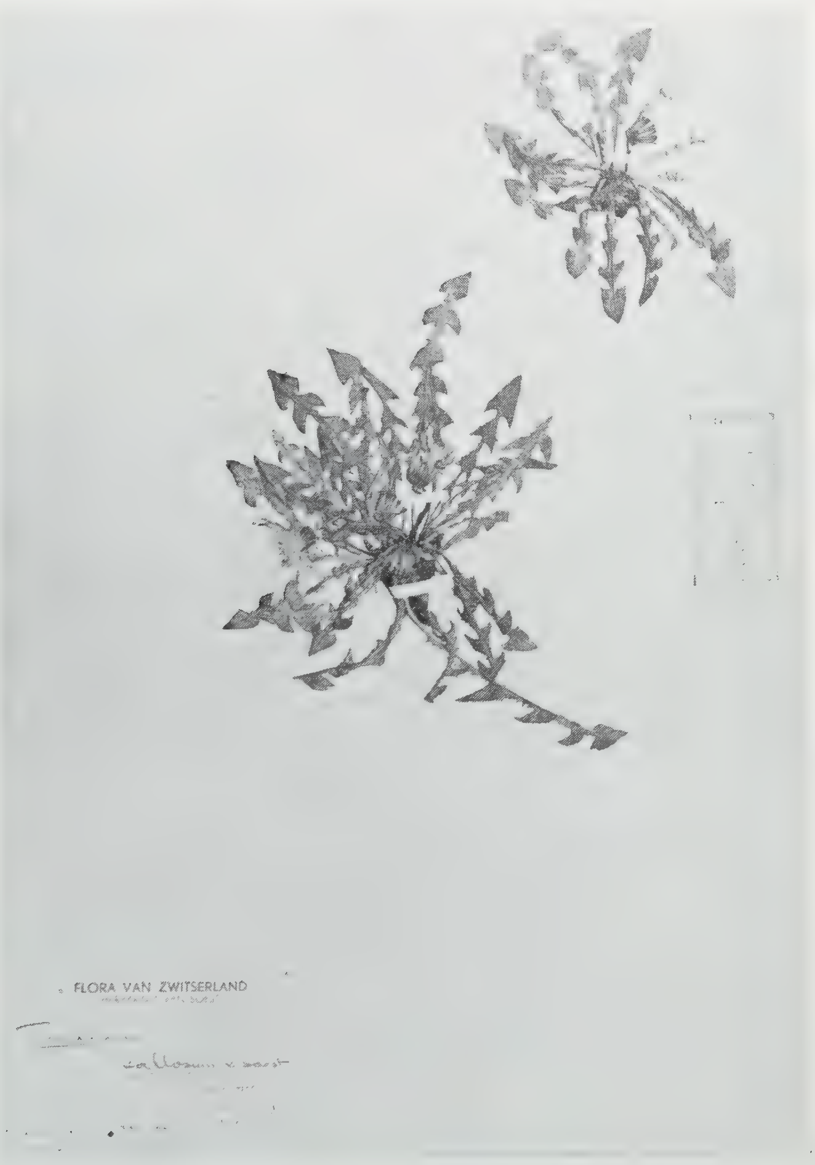

Fig. 23. T. callosum v.S., type specimen.

integro raro subgrosse dentato, interlobiis sublatiusculis ca. 2–3 mm latis saepe curvato- vel recto-dentatis vel denticulatis, interdum grosse, rarissime sublobato-dentatis; lobus terminalis subhastatus vel ± deltoideus vel subsagittatus, raro 1 dente munitus, lobuli basis acuti retroversi; petiolis brevis, 1–3 cm longis, subangustis vel subalatis, pallidis.

Scapi breves, sub involucro parce araneosi.

Involucrum mediocre ca. 1 cm latum, 1 cm longum, glauco-viride. Squamae exteriores laxe adpressae lanceolatae ad 5 mm longae, immarginatae; squamae interiores late lineares membranaceo-marginatae apice conspicue callosae.

Calathium planum radians, ad 3 cm diametro, dilute luteum. Ligulae marginales planae extus stria subpallide cano-purpurea notatae, apice interdum nigrescentes. Antherae polliniferae; styli lutei, stigmata sordide lutea. Floret aestate.

Achenium fulvo-stramineum parvum 3 mm longum (pyramide inclusa) superne spinulosum ceterum rugosum—basi laeve, in pyramiden brevam conicam 0,25 mm longam (spinulis saepe praeditam) inconspicue abiens. Rostrum ca. 5 mm longum; pappus albus, 4 mm longus.

E sectione Vulgariorum Dahlstedt.

Typus: Walliser Alp.: Saas–Fée, Fée–kessel 1800–2000 m, 7.7.1952 v. Soest (h. 31025–8); furthermore in the same valley: below Plattjen 22–2300 m, the achenes from this locality being used for the description; West slope of Mittaghorn 2100 m, 1952 v. S. (h).

3. **Taraxacum complicatum** van Soest **nov. spec.**

Planta sat humilis ad 10 cm alta, subgrosse araneoso-pilosa.

Folia numerosa ± decumbentia gramineo-viridia lobata petiolis nervoque mediano pallido; lobi laterales breves parvi falcati vel anguste triangulares saepe grosse dentati, acuti vel subacuti, interlobiis magis dentatis et denticulatis, angulis loborum saepe plicatulis interdum fusco-marginatis; lobus terminalis brevus sagittatus vel deltoideus subacutus, lobuli basis evoluti saepe dorso 1 dente munito.

Scapi pauci, foliis subaequilongi.

Involucrum (in formis alpinis minor) mediocre 12 mm longum, ad 14 mm latum crassiusculum, obscure viride. Squamae laeves, exteriores laxe adpressae ovatae 7 mm longae 4,5 mm latae pallide vel viride-marginatae ciliolatae; squamae interiores late lineares membranaceo-marginatae.

Calathium planum radians ad 3 cm diametro luteum, ligulae marginales planae extus stria cano-violacea notatae; antherae polliniferae, stylus luteus, stigmata livescentia; floret aestate.

Achenium (speciminis non typici) stramineum 4 mm longum (pyramide exclusa) superne spinulosum ceterum laeve, in pyramiden subcylindricam 0,7 mm longam abrupte abiens. Rostrum 6–7 mm longum, pappus albus 5 mm longus.

Typus: Rhaetische Alp.: Schlinigtal, near the Alp 1800 m, 12.7.1956 v. Soest (h. 36862; also 36861).

Furthermore:

Alp. de Savoie: Rochers d'Entre, 1920 Briquet (G).
Berner Alp.: Alpes de Bex, vallée de l'Avançon d'Anzeindaz, Le Dru 1895 m and Tortay 2340 m, 1943 Villaret (LAU).
Walliser Alp.: Almagelltal 24-2600 m, 1952 v.S. (h).
Bernina: Fextal, Marmorè 2100 m, 1923 Schibler (Z).

T. complicatum, especially in smaller forms growing at high altitudes, resembles species of sect. *Alpina* Hagl.; the outer bracts of the rather dark involucre are short indeed, but the achenes and their long rostrum show that this species belongs to sect. *Vulgaria* Dahlst.

4. **Taraxacum perfissum** van Soest **nov. spec.,** Fig. 24.

Planta mediocris 5–12 (–30) cm alta.

Folia numerosa decumbentia gramineo-viridia, inferne parce, in nervo dorsali densiuscule araneosa, petiolis angustis nervoque mediano pallido vel sordide rufescente. Folia exteriora oblanceolata ± lobata obtusa vel subobtusa; folia interiora ad 20 cm longa (petiolo inclusa) lingulata fissa; lobi laterales (ad 3 cm longi) lineares vel anguste triangulares erecto-vel ± reflexo-patentes vel falcati, acutissimi, paulo et saepe longe dentati, in interlobiis 1–1,5 cm longis valde longe subulato-dentatis (denti ad 1 cm longi) inconspicue abeuntibus; lobus terminalis sagittatus vel hastatus vel subtrilobatus acutus 1,5–2 cm longus, inferne ca. 2,5 cm latus, lobuli basis saepe lineares integri, lobulo apicali interdum dentato.

Scapi breves araneoso-pilosi.

Involucrum ad 15 mm longum, ad 20 mm latum. Squamae exteriores reflexo- vel erecto-patentes lanceolatae saepe elongatae ad 9 mm longae, subobscure virides, parum pruinosae apice ± purpurascentes, interdum inconspicue purpureo-marginatae, ciliolatae. Squamae interiores late lineares, inferne late membranaceo-marginatae.

Calathium ad 3 cm diametro, obscure luteum. Ligulae marginales planae extus stria cano-purpurea notatae. Antherae ± vacuae; stylus luteus, stigmata sordide lutea. Floret aestate.

Achenium 4 mm longum (pyramide inclusa) stramineum, superne squamuloso-spinulosum ceterum rugosum—basi laeve, in pyramiden conicam 0,6 mm longam abrupte abiens. Rostrum 9 mm longum; pappus ± sordide albus, 6 mm longus.

E sectione Vulgariorum Dahlstedt.

Typus: Silvretta: Alp Sardasca 1650 m, 22.7.1954 v. Soest (h. 33658); in the immediate neighbourhood furthermore: Vernelatal 2000–2200 m, Süsertal 2100 m, Vereinahaus 1950 m, Fremdvereina 1950 m, below Alp Sardasca 1550 m, all 1954 v. S. (h).

Furthermore:

Rhaetische Alp.: Dischmatal near Davos, 1899 Hegi (Z); Laret near Davos 1750 m, and Gotschnaboden 17–1800 m, both 1954 v.S. (h); Schlinigtal 1700–1750 m, 1956 v.S. (h).
Ortler: Martelltal 21–2300 m, 1956 v.S. (h).

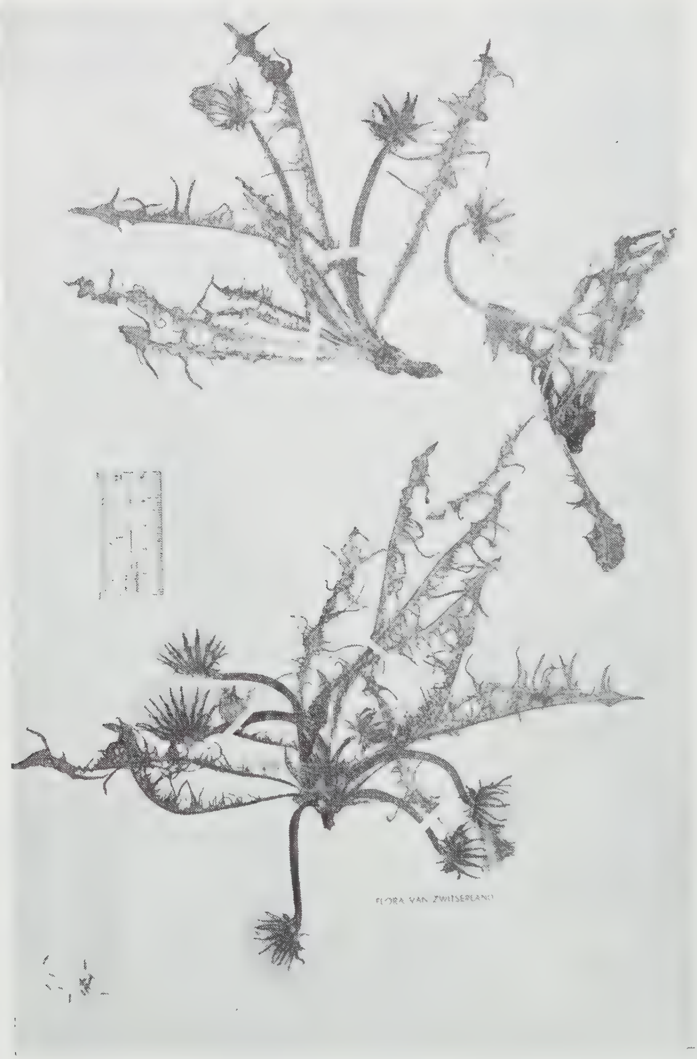

Fig. 24. T. perfissum v.S., type specimen.

5. **Taraxacum praeticum** van Soest **nov. spec.,** Fig. 25.

Planta 25 cm alta inferne glabra.

Folia suberecta gramineo-viridia nervo mediano subaraneosa, petiolis roseo-purpureis dentibus filiformis munitis, pro parte subalatis. Folia interiora ad 20 cm longa (petiolo inclusa), lobata; lobi laterales utrinque 3–4, falcati acutissimi e basi lati, patentes vel erecto-patentes, dorso saepe longe dentati vel denticulati, ± abeuntes in interlobiis latiusculis (5–10 mm) et longis; lobus terminalis magnus

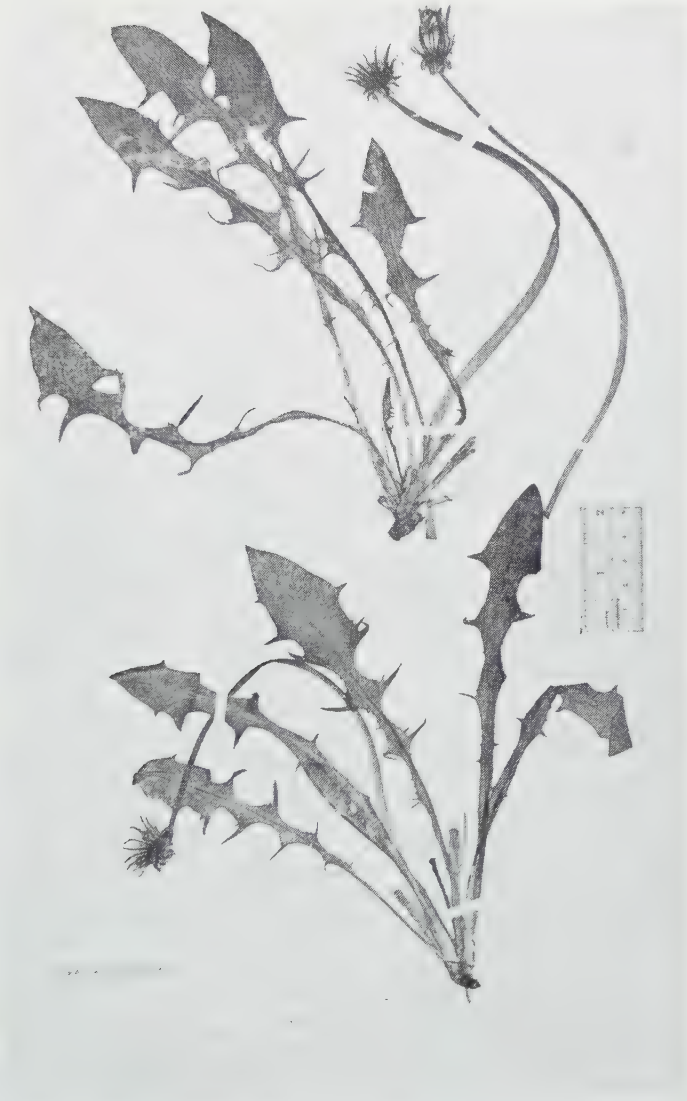

Fig. 25. T. praeticum v.S., type specimen.

ad 4 cm longus, 1,5–2,5 cm latus subacutus saepe sublobatus vel paulo patente dentatus, longe hastatus vel ± ovatus vel ovato-triangularis vel subsagittatus; lobuli basis falcati dorso saepe magis dentati vel pseudo-fissi. Folia exteriores oblongo-lanceolata subintegra, dentata vel sublobata.

Scapi colorati sub involucro subdense araneosi.

Involucrum mediocre 17 mm longum, angustum (ca. 12 mm latum) obscure viride. Squamae exteriores reflexo-patentes denique retroflexae, lanceolatae ca. 9 mm longae, immarginatae vel pro parte inconspicue purpureo-marginatae; squamae interiores late lineares membranaceo-marginatae, omnes ± purpureae.

Calathium planum radians ad 3 cm diametro ± croceum. Ligulae marginales extus stria obscure purpurea ornatae. Antherae polliniferae; stylus et stigmata sordide lutea siccis subnigra. Floret aestate.

Achenium parvum 2,7 mm longum (pyramide exclusa) superne spinulosum ceterum rugosum—basi laeve, in pyramiden 0,4 mm longam subabrupte abiens. Rostrum 9 mm longum; pappus niveus 5 mm longus.

E sectione Vulgariorum Dahlstedt.

Typus: Rhaetische Alp.: Klosters, below Pardenn 1320 m, 14.7.1954 v. Soest (h. 33636–7).

Furthermore:

Berner Alp.: Alpes de Bex, La Varraz 1800 m, 1942 Maillefer (LAU).

Rhaetische Alp.: Klosters 1300 m, Mönchalptal 1450 m, Rüti 1450 m and below Gotschna 1750 m, all 1954 v.S. (h).

Silvretta: between Monbiel and Vereina 1300 m, Sardascatal 1300 m and Vereinahaus 1950 m, all 1954 v.S. (h).

Hohe Tauern: Granatspitzgruppe, Muntanitz 2450 m, 1952 Wendelberger (h. Melzer).

6. **Taraxacum reophilum** van Soest **nov. spec.,** Fig. 26.

Planta gracilis ca. 15–30 cm alta, valde glabrescens.

Folia suberecta luteo-viridia vel paulo canescentia, petiolis pallidis anguste alatis; folia interiora ca. 20 cm longa, lobata; lobi laterales utrinque 4–5 ,lanceolati vel anguste triangulares acuti erecto- vel reflexo-patentes integri vel dorso rarissime denticulati vel dentati, angulis loborum superiorum plicatis; interlobiis longis (ad 3 cm) latiusculis (0,5–1 cm) raro integris interdum denticulatis, saepe longe patento-dentatis vel lobulis lanceolatis ad 8 mm longis munitis; lobus terminalis ± sagittatus, lobuli basis retroflexi vel saepissime patentes, acuti, lobulo apicali elongato saepe subobtuso, omnes integri vel parce denticulati.

Scapi floriferi foliis aequilongi vel eis breviter superantes, sub involucro araneosi vel glabrescentes.

Involucrum 1,5 cm longum, 1,5 cm latum, basi rotundatum, subobscure viride glaucescens. Squamae exteriores laxe adpressae ovatae vel ovato-lanceolatae, ad 6 mm longae, ad 3 mm latae, acuminatae summo obtuso, apice parum marginatae; squamae interiores late lineares membranaceo-marginatae.

Calathium planum radians ad 3 cm diametro, ± croceum. Ligulae marginales planae extus stria pallide cano-purpurea notatae. Antherae polliniferae; stylus luteus; stigmata sordide lutea, denique subobscura. Floret aestate.

Achenium 5 mm longum (pyramide inclusa) stramineum superne tuberculatum vel brevissime spinulosum, ceterum laeve, in pyramiden

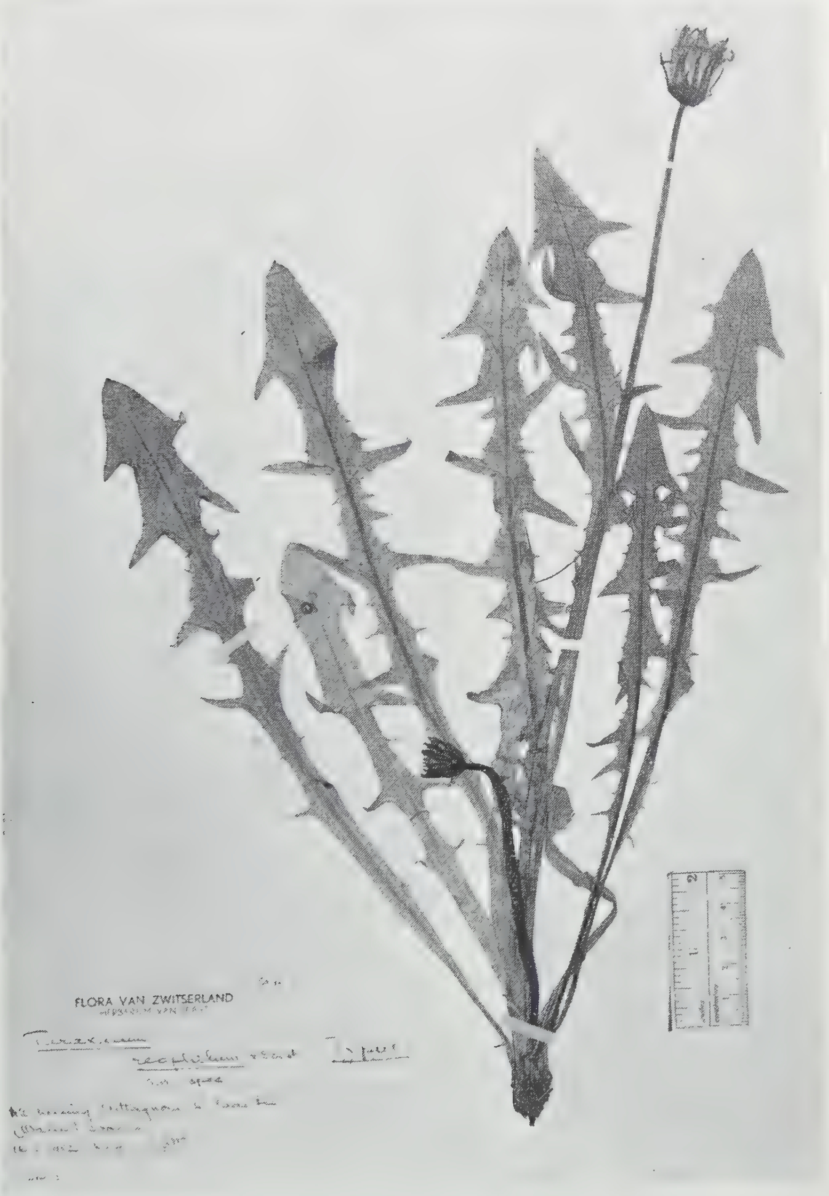

Fig. 26. T. reophilum v.S., type specimen.

conicam sublongam (0,7 mm) subsensim abiens. Rostrum breve, 5–6 mm longum; pappus albus 5 mm longus.

E sectione Vulgariorum Dahlstedt.

Typus: Walliser Alp.: Saas–Fée, northwest slope of Mittaghorn 2000 m, along brooklets, 16.7.1952 v. Soest (h. 31064–71); in the neighbourhood: Saas–Fée 18–2000 m, below Mittaghorn at 1800 m, towards Saas–Almagell 1800 m, near Mattmark 2000 m, all 1952 v. S. (h).

Furthermore:

Walliser Alp.: Steinental near Bérisal, 1893 Chenevard (G).
Berner Alp.: Alpes de Bex, Les Ayers 1870 m, 1946 Maillefer (LAU).
Rhaetische Alp.: Schlappintal near Klosters 1600 and below Gotschna 1300 m, both 1954 v.S. (h).
Silvretta: Vernelatal 2100 m, 1954 v.S. (h).
Oetztaler Alp.: Radurscheltal near Pfunds, 1926 Vetter (W) and 1936 Plank (W).
Ortler: Martelltal 21–2300 m, 1956 v.S. (h).
Vorarlberg: Solarneljoch, Scesaplana, 1912 Vetter (W).
Hohe Tauern: Kals 1900 m, 1931 H.M. (W).

This species can be considered as a link between the *Vulgaria* and the *Fontana*; it seems to be related to *T. aestivum* m, from which it differs by a shorter rostrum. The dark colour of the flower heads indicates the affinity to the *Fontana*.

7. **Taraxacum rhaeticum** van Soest **nov. spec.,** Fig. 27.

Planta mediocris 5–15 cm alta.

Folia suberecta ad 17 cm longa (petiolo angusto pallido inclusa), araneosa, lobata; lobi laterales utrinque 4–6, angusti acuti unguiculosi, falcati summo retroverso vel retroflexo, integri vel inferiora saepe magne dentati vel interdum fissi et multidentati; interlobiis interdum dentatis saepe 3 mm latis, in folia exteriora 5–15 mm longis, in folia interiora saepe subnullis; lobus terminalis deltoideus vel hastatus vel subsagittatus subacutus, lobuli basis acuminati integri, lobulo apicali saepe longe lingulato ad 2 cm lato, integro vel interdum paulo crispato-denticulato.

Scapi floriferi foliis breviter superantes, sub involucro araneosi vel glabrescentes.

Involucrum mediocre 12 mm longum, ca. 12 mm latum saepe crassiusculum. Squamae exteriores erecto-patentes apice recurvatae, ovatae vel ovato-lanceolatae ad 7 mm longae 2-3 mm latae, saepe pallide virides purpurascentes, sublate albo- vel purpureo-marginatae. Squamae interiores late lineares membranaceo-marginatae.

Calathium paulo radians ad 2,5 cm diametro. Ligulae luteae, marginales angustae extus stria purpurea notatae; antherae vacuae; stylus et stigmata lutea; floret in regionis alpinis aestate, in regionis subalpinus interdum vere.

Achenium stramineum 4 mm longum (pyramide inclusa) superne breve spinulosum (spinulis ± rufescentis), ceterum sublaeve, in

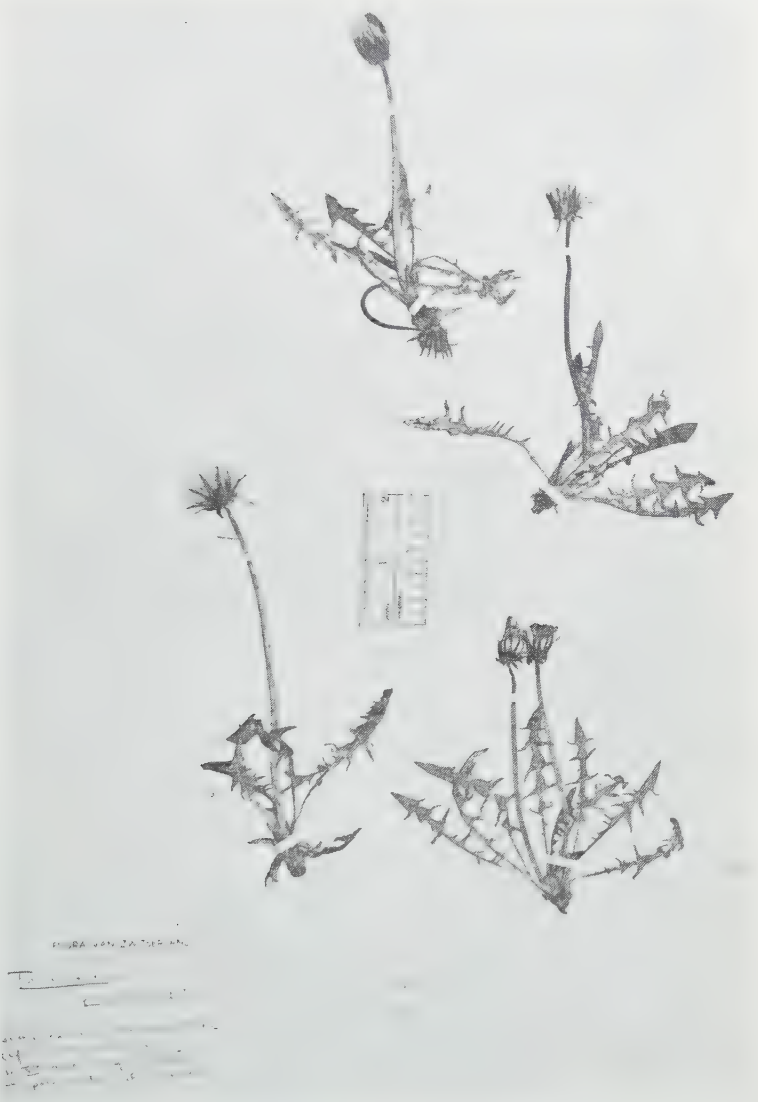

Fig. 27. T. rhaeticum v.S., type specimen.

pyramiden conicam 0,5 mm longam spinulis saepe praeditam sensim abiens; rostrum 7 mm longum; pappus albus 6 mm longus.

E sectione Vulgariorum Dahlstedt.

Typus: Rhaetische Alp.: Albula road below Naz 1550–1650 m, 10.7.1948 v. Soest (h. 19285, 19287); furthermore very common in the neighbourhood: Albula pass, abundant 21–2300 m, Albula

Hospiz 2300 m, Weissenstein 2050 m, Preda–Palpuogna 1850 m, Naz–Bergün 1400-1630 m abundant, Val da Munz 1600 m, Val Tuors 1600 m, Bergün–Bergünerstein 1350–1400 m, all 1948 v. S. (h).

Furthermore:

Walliser Alp.: Saastal, Mattmark 2100 2150 m; im Lerch 1900 m and Hannigalp near Saas-Fée 22–2400 m, all 1952 v.S. (h); Col de Torrens 28–2900 m, 1919 Gandoger (RUEB); Riffelalp 2200 m, 1947 Horn af Rantzien (S).

Berner Alp.: Alpes de Bex, Col des Essets 2000 m, 1905 Wilczek (LAU); Gletscheralp, Loetschental, 1939 Weibel (G); Sigreswiler Grat 1820 m, 1933 Lüdi (ZT).

Vierwaldstädter Alp.: Kartigel, Meiental 1350 m, 1914 E. Schmid (Z).

Glarner Alp.: Calanda, Ziegler (LAU).

Rhaetische Alp.: Klosters, forest 1250–1300 m, Klosters-Laret 1400 m, above Laret 1600 m, Mönchalptal 1300 m, Klosters-Serneus 1200 m, Landquart valley near Alp Pardenn 1320 m, Stutzbachtal below Pardenn 1900 m and Parsenn 22–2400 m, all 1954 v.S. (h); Aelpli, Arosa 2100 m, 1898 Chenevard (G); Schlinigtal, 1956 v.S. (h).

Bernina: pass 2050–2250 m, 1948 v.S. (h).

Silvretta: Schlappintal 1400 m, 1500 m and 1600 m, all 1954 v.S. (h).

Ortler: Martelltal 2350 m, 1956 v.S. (h).

Oetztaler Alp.: Matschertal 1600–1650 m and Prossental 1900 m, 2000 m and 21–2200 m, all 1956 v.S. (h).

8. **Taraxacum serpentinum** van Soest **nov. spec.,** Fig. 28.

Planta 7–15 cm alta glabrescens.

Folia numerosa suberecta gramineo-viridia vel sublutescentia, nervo mediano ± araneoso-pilosa, petiolo pallide purpureo-colorato. Folia exteriora breve lobata, lobi laterales ± dentati; lobus terminalis ± hastatus acuminatus. Folia interiora ad 18 cm longa (petiolo subalato inclusa); lobi laterales utrinque 4–5, triangulares vel ± falcati saepe angusti acuti summo pro max. parte retroverso, dorso convexo vel recto dentati vel inciso-dentati vel denticulati, margine inferiore saepe recto integro; interlobiis 2–3 mm latis saepe ad 1 cm longis dentatis; lobi laterales superiores approximati; lobus terminalis ± hastatus vel plerumque trilobatus, lobuli basis triangulares summo valde elongato saepissime retroverso acuto, dorso valde convexo subintegro, lobulo apicali pro max. parte anguste lineare vel longe deltoideo, 1–3 mm lato, ca. 5 mm longo, acuto.

Scapi foliis aequilongi vel eis breviter superantes, sub involucro ± araneosi.

Involucrum viride ± crassiusculum 13 mm longum 16 mm latum. Squamae exteriores patentes apice recurvatae lanceolatae ad 7 mm longae, ad 2,5 mm latae immarginatae obtusae apice ciliolatae; squamae interiores lineari-lanceolatae membranaceo-marginatae.

Calathium valde radians ad 3,5 cm diametro. Ligulae saturate luteae marginales planae vel subplanae, extus stria purpurea paulo notatae, apice saepe obscure purpureae. Antherae vacuae vel parce polliniferae; styli et stigmata sordide lutea. Floret aestate.

Achenium stramineum 4 mm longum (pyramide exclusa) superne spinulosum ceterum tuberculatum—basi laeve, in pyramiden conico-cylindricam 0,8 mm longam subsensim abiens; rostrum 5–6 mm; pappus albus 5–6 mm longus.

E sectione Vulgariorum Dahlstedt.

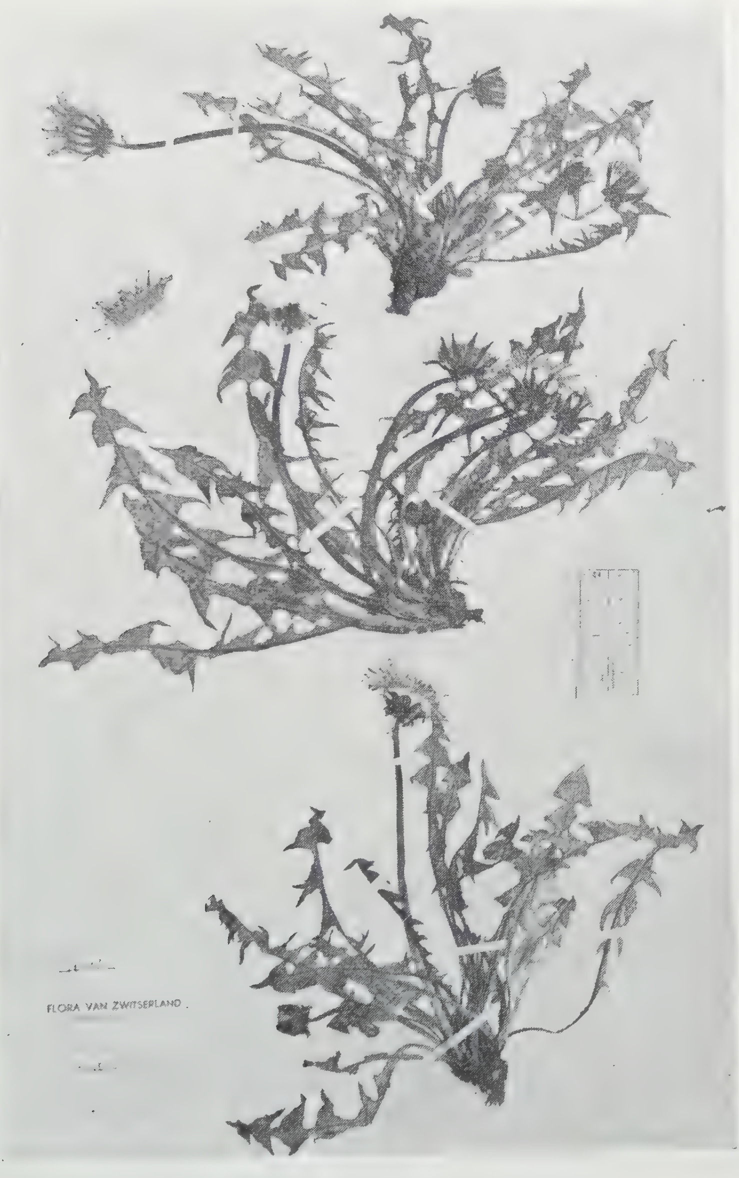

Fig. 28. T. serpentinum v.S., type specimen.

Typus: Rhaetische Alp.: Parsenn, Stutzbachtal 1800 m on serpentine, 21.7.1954 v. Soest (h. 33659), also no. 33655.

Furthermore:

Rhaetische Alp.: Albula, Val Tisch 1850–2100 m, 1948 v.S. (h).

SUMMARY

In sect. *Ceratophora* Dahlst. *T. krättlii* (Piz Padella) is described.

In sect. *Alpina* Hagl. a number of new sp. are described, a few only restricted to the western^{+} or to the eastern^{++} Alps: *T. carinthiacum* (also western Balcans), *T. helveticum* (also Tatra) with f. *lobatum*, *T. mattmarkense*$^{+}$, *T. panalpinum* (also high mountains in Spain, Tatra and Transsilvanian Alps, western Balcans), *T. parsennense*$^{++}$, *T. pseudofontanum*, *T. saasense*$^{+}$, *T. vereinense*, *T. vernelense*$^{++}$, *T. vetteri.* The latin description of 2 already known sp. is enlarged: *T. apenninum* (Tenore) DC. em v.S. (Apennines) and *T. petiolulatum*$^{++}$ (Huter) v.S. nov. comb.; furthermore *T. oreophilum* Hagl. and *T. venustum* Dahlst.$^{++}$ are treated.

In sect. *Fontana* nov. sect., next to *T. fontanum* H.M. sens. str., a number of new species are described: *T. aurantellum*$^{++}$, *T. corsicum* (Corse), *T. fontanicolum*$^{++}$ (also Tatra), *T. fontanosquameum*$^{++}$, *T. peralatum*$^{++}$, *T. pohlii*$^{++}$, *T. pseudoboreigenum* (Central Alps). In connection with this section *T. aestivum*$^{++}$ and *T. crocellum*$^{++}$ are described.

In sect. *Cucullata* nov. sect., besides *T. cucullatum* Dahlst. and *T. tiroliense* Dahlst., *T. fontaniforme* (Bernina) is described.

In connection with sect. *Rhodocarpa* v.S. (*T. schroeterianum* H.M.), *T. rufocarpum* is described (Alps, W. Balcans).

In sect. *Vulgaria* Dahlst. the following sp. are described: *T. aequilobiforme*$^{+}$, *T. callosum*$^{+}$, *T. complicatum*$^{+}$ (also Bernina), *T. perfissum*$^{++}$, *T. praeticum*, *T. reophilum*, *T. rhaeticum*, *T. serpentinum* (central Alps).

Photographs of the type specimens of most of the new sp. are published.

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NOTES ON THE ARACEAE OF SURINAME II[1]

A. M. E. JONKER–VERHOEF AND F. P. JONKER

(*Botanical Museum and Herbarium, Utrecht*)

(*received February 11th, 1959*)

After the publication of the *Araceae* in the Flora of Suriname I.2 (1953), p. 1–80, a number of rare and new species have been collected. Some of these were collected by Dr. J. Lindeman between 1953 and 1955, the remaining by the present authors, who visited Suriname from November, 1955, to March, 1956. Field observations by the authors clearly indicated the fragmentary status of our knowledge of Suriname Aroids. The reasons for this are to be sought in the difficulties involved in collecting and preserving. Also, a number of species may not flower over a period of several years. The inflorescences of many lianas are often almost inaccessible. A source of confusion is the variability in the leaves of a species.

The following is an enumeration of species collected for the first time in Suriname, in addition to records of re-collections of rare species.

Anthurium Schott

1. *Anthurium crassinervium* (Jacq.) Schott, a species already listed in Fl. of Sur. and known only from the interior, was collected for the third time:

Marowijne Riv., Nassau Mts., frequent in forest on bauxite, alt. 550 m (Cowan & Lindeman 39100, fl. Jan. 1955 [NY, U]).

In Fl. of Sur. we described this species as a terrestrial, rosulate herb. It is recorded by Cowan and Lindeman as epiphytic. According to their field notes the spathe is dark red; the spadix is purple black.

2. *Anthurium andersonii* Schott. The species is new for Suriname. The specimens were collected as long ago as 1926. The material had been mislaid in the Utrecht herbarium and, for that reason, was not listed in Fl. of Sur.

Anthurium andersonii Schott in Oest. Bot. Wochenbl. (1857), p. 325; Schott, Prod. Syst. Aroid. (1860), p. 547; Griseb., Fl. Br. W. Ind. Isl. (1864), p. 509; Engler in DC., Mon. Phan. Prod. II (1879), p. 207; Engler in Das Pflanzenreich IV 23B (1905), p. 286; – *A. digitatum* (Jacq.) G. Don var. *connatum* Engl. in Engl., Bot. Jahrb. XXV (1898), p. 457.

Climber; internodes up to 2 cm long. Petiole sulcate, ca. 63 cm long and 0.5 cm in diameter; sheath ca. 8 cm long; joint ca. 3 cm long, forking in the pedate leaf base. Leaf blade subdigitately pedate, 7- to 11-foliolate; the two outer leaflets connate with the neighbouring ones in the basal 7 cm. Leaflets pergameneous, sessile, entire, oblanceolate, cuspidate, cuneate at the base, 29–46 cm long and 3–10 cm wide. Outer leaflets shorter than the others; their midribs, on the outer side, denudate in the basal 3–4 cm; the 8 cm long part of the blade above the denudate part broadened in its exterior half. Peduncle slender, ca. 22 cm long. Spathe lanceolate, ca. 2.5 cm wide. Spadix sessile, dark red-brown, cylindrical, ca. 9 cm long and up to 1 cm in diameter. Tepals cucullate, ca. 3 mm long, width of the outer ones ca. 2 mm; of the narrower inner ones ca. 1.5 mm. Stamens ca. 1.6 mm long and 0.7 mm wide. Ovary cylindrical, 2-locular, ca. 2 mm long and 1 mm in diameter, crowned by a rounded stigma; each locule containing a single ovule.

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[1] Part I appeared in Acta Botanica Neerlandica Vol. 2(3), Oct. 1953, p. 349–362, and was also published as Mededelingen van het Botanisch Museum en Herbarium van de Rijksuniversiteit te Utrecht, no. 118.

Distribution: West-Indian Islands (Sta. Lucia, Guadeloupe, Martinique,? Tobago).

Upper Gran Rio, common (Stahel 241, fl. March 1926 [U]).

Heteropsis Kunth

Heteropsis longispathacea Engl. was collected for the second time. The plants were climbing against tree trunks and rooting at the nodes.

Upper Nickerie Riv., right bank, camp Powiesi Boutoe (Jonker 404, ster. Jan. 1956 [U]).

Another species, probably belonging to this genus, has now been collected four times in Suriname, but never in fertile state. It is not impossible, however, that the material represents *H. longispathacea* Engl. in a juvenile state. It differs by its much longer leaf sheath (1.5–2.5 cm) and its much finer venation.

Marowijne Riv., Wane creek (Lanjouw & Lindeman 538, ster. Sept. 1948 [U]); Suriname Riv., between Joden Savanne and Mapane creek (Lindeman 5198*a*, ster. Dec. 1953 [U]); Upper Nickerie Riv., camp Powiesi Boutoe (Jonker 406, ster. Jan. 1956 [U]); id., Anjoemara creek (Jonker 435, ster. Jan. 1956 [U]).

Dieffenbachia Schott

Dieffenbachia paludicola N.E.Br. ex Gleas. was known from British Guiana and twice collected in Suriname. According to our observations the species is not very rare. It occurs along springs on peaty soil.

Zanderij, forest near Matta (Lindeman 6516, fl. Aug. 1954 [U]); id., Pontji creek, path to Matta (Jonker 137, fr. Dec. 1955 [U]).

Vernacular names, added to those mentioned in Fl. of Sur.: pingotajer, watradonké, water-dontje.

Xanthosoma Schott

1. *Xanthosoma conspurcatum* Schott. This species had been collected only once, near Paramaribo, by Wullschlaegel (type collection). We discovered a rich locality near Albina. Our description in Fl. of Sur. has to be altered in the following way.

Terrestrial, rosulate plants, up to 1 m high, containing a milky uice; underground part not tuberous. Cataphylls linear-lanceolate, membranous, 12–17 cm long and 1–1.5 cm wide. Petiole vaginate in the basal part, 39–75 cm long, provided with scattered, indistinct, white stripes; sheath 11–33 cm long and 2–3 cm wide. Leaf blade ovate, cordate to hastate at the base, acuminate at the apex, 19–45 cm long and 7.5–35 cm wide between the basal lobes, dark green above, light green beneath, white-spotted on both sides. Apical lobe 6.5–26 cm wide; basal lobes obtuse, up to 24 cm long and 13 cm wide; sinus rounded, penetrating to the main ribs of the basal lobes; denudate part of the mains ribs 0.5–2 cm long. Peduncle terete, 13–36 cm long. Spathe 15–17 cm long, basal tubular part 4–7 cm long, green outside; limb broadly elliptical, acute, 6–9 cm long and up to 4 cm wide, white to cream-coloured on both sides. Spadix shortly stipitate; stipe adnate to the spathe. Basal, female part ca. 1.5 mm long, its basal part adnate to the spathe; ovaries shortly ovoid, ca. 1 mm high, 3- to 4-locular, crowned by a broad, discoid style and a semiglobose stigma. Basal half of the 3.5 cm long sterile part provided with rather large, 4 mm high, 6-angular, prominent synandrodia, 2–3 mm in diameter; apical half of the sterile part provided with elongate, 6-angular, appressed synandrodia, 0.5 mm high, 5 mm long and 1 mm wide. Male part clavate, ca. 5 cm long; synandria 1.5 mm high and 1.5–2 mm in diameter.

Distribution: Endemic.

Near Paramaribo (Wullschlaegel 501 [BR], type); Lower Marowijne Riv., N of Albina, Pierre Kondre (Jonker 377, fl. Jan. 1956 [U]).

2. *Xanthosoma hoffmannii* (Schott) Schott was collected by us for the first time in Suriname. It differs from the related *X. helleborifolium* (Jacq.) Schott chiefly in the leaves which are not compound and pedate but pedatifid and consisting of 5–9 divisions. The latter are much broader than the, usually 11, leaflets of *X. helleborifolium*.

Xanthosoma hoffmannii (Schott) Schott in Oest. Bot. Ztschr. XV (1865), p. 33; Engler in Mart., Fl. Bras. III. 2 (1878), p. 191; id., in DC., Mon. Phan. Prod. II (1879), p. 485; Hemsley, Biol. Centr. Am. Bot. III (1885), p. 418; Engler u. Krause in Das Pflanzenreich IV 23E (1920), p. 60; — *Acontias hoffmannii* Schott, Prod. Syst. Aroid. (1860), p. 196; Ørst., Praecurs. Fl. Centroam. (1873), p. 55.

Terrestrial herb. Petiole vaginate, pubescent in the basal part, up to 45 cm long, flattened towards the apex; sheath gradually narrowed in the petiole, up to 12 cm long and 2 cm wide. Leaf blade herbaceous, reniform in outline, 17 cm long and 26–29 cm wide, pubescent above, along the margin and on the veins beneath, pedatifid into 5–9 divisions. Rachis not naked between the "leaflets"; the latter obovate to oblong, entire, apiculate, mucronate, 6.5–16 cm long and 2.5–7.5 cm wide. Peduncle terete, slightly pubescent, 26–27 cm long. Basal, tubular part of the spathe coriaceous, green, 6–7 cm long and up to 3.5 cm in diameter; limb herbaceous, lanceolate, acuminate, 9–10 cm long and up to 2.5 cm wide, yellow with pink margin outside, yellowish-white inside. Spadix narrowly cylindrical, stipitate; stipe ca. 0.5 cm long. Female part ca. 2 cm long and 1 cm in diameter, covered with yellow slime; ovaries 3-locular, 1.5 mm high and 1.2 mm in diameter; placentas axile with 4 ovules above each other. Style discoid, 0.5 mm high and 1.5 mm in diameter; stigma semiglobose, 1.2 mm in diameter. Sterile part narrowed towards its apex, 4 cm long and 7.5–10 mm in diameter, cream-coloured at the base, white towards the apex; synandrodia oblong, 10–15 mm long and 2-3 mm wide. Male part clavate, cream-coloured, 6 cm long and 7.5 mm in diameter; synandria 4 mm long, 1.5 mm wide and 2.5 mm high, consisting of ca. 13 anthers.

Distribution: Mexico, Costa Rica, Guatemala.

var. *wendlandii* (Schott) Engl. in Mart., Fl. Bras. III. 2 (1878), p. 191; id. in DC., Mon. Phan. Prod. II (1879), p. 485; Hemsley, Biol. Centr. Am. Bot. III (1885), p. 418; Engler u. Krause in Das Pflanzenr. IV 23E (1920), p. 60; — *Acontias wendlandii* Schott in Oest. Bot. Ztschr. VIII (1858), p. 178; id., Prod. Syst. Aroid. (1860), p. 195; Ørst., Praecurs. Fl. Centroam. (1873), p. 54; — *Xanthosoma wendlandii* (Schott) Standl., Fl. Costa Rica in Field Mus. Nat. Bot. Ser. XVIII (1937), p. 145.

Basal part of the petioles and sheaths provided with red stripes. Leaves dark green above, variegated with light green, light green beneath.

Distribution: Costa Rica.

Paramaribo, road to Leonsberg (Jonker 520, fl. Feb. 1956 [U]).

It is rather difficult to identify the cultivated Xanthosomas, generally known as "tajer", especially as they flower rarely. Engler, in "Das Pflanzenreich", mentions for Guiana: *X. sagittifolium* (L.) Schott, *X. caracu* C. Koch et Bouché and *X. belophyllum* (Willd.) Kunth, all three cited by us in Fl. of Sur. In our opinion, after study of the fresh material, the "tajers" sold on the markets as leafy vegetables or edible tubers are cultivars of *X. sagittifolium* (L.) Schott. We think it highly probable that both *X. belophyllum* (Willd.) Kunth and *X. caracu* C. Koch et Bouché belong to *X. sagittifolium*. The flowers of *X. caracu* have never been described. The differences between the three species are based on the leaf shapes which fall within the width of variation of *X. sagittifolium*.

3. *Xanthosoma sagittifolium* (L.) Schott; vid. Fl. of Sur. I. 2, p. 53. Plants up to 3 m high, often with milky juice; large specimens sometimes provided with a short, thick, aerial stem. Rhizome often elongate-tuberous, ca. 10 cm in diameter. Cataphylls membranous, linear, acute. Leaves rosulate, petiolate. Petiole vaginate in the basal part, up to 2 m long; sheath gradually narrowed into the petiole. Leaf blade herbaceous to subcoriaceous, sagittate to cordate, sometimes slightly hastate, up to 1 m long, acuminate and mucronate at the apex; basal lobes obtuse; sinus parabolic, not penetrating to the main ribs of the basal lobes. Peduncle terete, bluish-green, 20–25 cm long and 1 cm in diameter. Spathe ca. 20 cm long; tube coriaceous, closed, green, ca. 10 cm long and 2.5 cm in diameter; limb enclosing the flowering spadix, lanceolate, acuminate, ca. 10 cm long and 4 cm wide, 3-costate on the back, outside light green, inside cream-

coloured. Spadix up to 13 cm long, obliquely sessile. The basal, female part swollen, ca. 4 cm long and 2.8 cm in diameter; ovaries cylindrical, ca. 1.5 mm high, 3-locular, crowned by a lobate, flat stigma, ca. 1.5 mm in diameter. Sterile part cylindrical, 3–4 cm long and 0.8 cm in diameter, provided with a basal whorl of slender, erect appendages (pistillodes?), up to 6 mm long, and ca. 10 remote whorls of peltate synandrodia, gradually growing more elongate towards the apex. Male part ca. 6 cm long, acute, in the basal part provided with whorls of synandria consisting of a peltate central column with ca. 5 adnate stamens. Towards the apex the peltate central part of the synandria gradually becoming reduced and, sometimes, appearing as a sterile pistil. Apical part of the spadix covered with a dense mass of stamens which are gradually elongated towards the apex.

A cultivar often grown for the edible rhizomes is known as "pom tajer". It may rapidly develop into a very large plant provided with large leaves and forming a short, thick stem in the next years. Inflorescences are rather rare, however, as the plant is, in culture, harvested before producing flowers.

Lower Coppename Riv., Boskamp (Jonker 401, fl. Jan. 1956 [U]); Paramaribo, Tourtonnelaan (Jonker 681, fl. March 1956 [U]); Marowijne Riv., Nassau Mts., alt. 415 m, in clearing (Cowan & Lindeman 39082, fl. Jan. 1955 [NY, U]).

Another cultivar, grown everywhere as a leafy vegetable is known as "tajerblad", "taja wirie", etc. The bundled leaves are sold. It is a much smaller herb, up to 50 cm high, provided with rosulate, herbaceous leaves. It has never been collected in flower and consequently it is unknown whether it has to be considered a juvenile or undeveloped form of the previous cultivar. To this cultivar belongs the specimen from herb. Hermann, cited by us in Fl. of Sur. as *X. belophyllum* (Willd.) Kunth.

Paramaribo, market (Jonker 273, 275 [U]); Coronie, Agricultural Experiment Fields (Jonker 558 [U]).

4. *Xanthosoma jacquinii* Schott, Melet. I (1832), p. 19; id., Syn. Aroid. (1856), p. 57; id., Prod. Syst. Aroid. (1860), p. 183; Engler in Mart., Fl. Bras. III. 2 (1878), p. 169; id. in DC., Mon. Phan. Prod. II (1879), p. 470; Hemsley, Biol. Centr. Amer. Bot. III (1885), p. 418; Engler u. Krause in Das Pflanzenreich IV 23E (1920), p. 47; Simmonds in Kew Bull. 1950 (1951), p. 400; — *Xanthosoma maximiliani* Schott in Bonplandia X (1862), p. 322; Engler in Mart., Fl. Bras. III. 2 (1878), p. 192; Schott in Peyritsch, Aroid. Maxim. (1879), p. 42, tab. 31–33; Engler in DC., Mon. Phan. Prod. II (1879), p. 470; Engler u. Krause in Das Pflanzenreich IV 23E (1920), p. 49.

Plant up to 3 m high; milky juice evil-smelling; large specimens provided with an aerial stem which is up to 1.5 m high and 20 cm in diameter. Rhizome tuberous, brownish-black outside, inside white. Petiole terete, up to 1.5 m long, vaginate in the basal part. Leaf blade herbaceous to subcoriaceous, broadly cordate, often slightly hastate, ca. 80 cm long and 60 cm wide; acuminate and mucronate; margin slightly undulate; basal lobes angular, obtuse, in larger leaves usually overlapping; midrib of the basal lobes exposed in the sinus over 2–3 cm. Peduncle 20–40 cm long and 0.5 cm in diameter. Spathe ca. 19 cm long; tube coriaceous, green, closed, 6.5 cm long and 3.5 cm in diameter; limb herbaceous, enclosing the flowering spadix, white, crimson-purple within at base, 12.5 cm long and 6 cm wide. Spadix stipitate, up to 15 cm long, green; stipe 1 cm long, adnate to the spathe. Female part slightly swollen, ca. 1.5 cm long and 1 cm in diameter; ovaries cylindrical, ca. 2 mm high, 3- to 4-locular, crowned by a disciform, 0.5 mm high style which is 8 mm in diameter. Sterile part rose-coloured, swollen at the base and constricted in the apical part, 4.5 cm long; basal swollen part 1.3 cm in diameter, provided with large synandrodia which are 6 mm in diameter and 6 mm high; apical part provided with smaller synandrodia which are diminishing and narrower towards the apex; apical synandrodia ca. 3 mm high, 5 mm long and 2 mm wide. Male part ellipsoid, ca. 6.5 cm long and 0.8 cm in diameter, cream-coloured to flesh-coloured; synandria 3 mm high and 3 mm in diameter, consisting of ca. 6 stamens. Fruit baccate, up to 1 cm long and 0.5 cm in diameter.

Distribution: S. Florida, West-Indian Islands, Central America, tropical South America; also cultivated.

Lower Suriname R., plant. Peperpot (Lindeman 3694, fl. Apr. 1953 [U]); Coronie, Leasowes, near Sarah lake (Jonker 550, ster. March 1956 [U]).

Vernacular name: tajer.

Apparently this species is only rarely cultivated in Suriname. We were told in Coronie that the tubers were edible and that the leaves were eaten too. Sometimes, however, the leaf appears too acrid for human food; then they are used as pig's wash. According to Engler and Krause (1920) the species is widely cultivated in the tropics of both hemispheres. According to Simmonds (1951) it is, in Trinidad and Tobago, a good wild species that is never cultivated and, according to local tradition, poisonous.

Other species grown for human food are: *X. violaceum* Schott, *X. atrovirens* C. Koch et Bouché, *X. mafaffa* Schott, *X. brasiliense* (Desf.) Engl. We did not observe cultures of these species in Suriname. The vernacular name "tajer" is also applied to *Colocasia esculenta* (L.) Schott.

Caladium Vent.

1. *Caladium schomburgkii* Schott, hitherto known from French and British Guiana only, was collected near Albina, where it occurred abundantly. Because of its white-veined leaves the Suriname material belongs to the var. *argyroneurum* (C. Koch) Engl.

Lower Marowijne Riv., N of Albina, (Jonker 374, fl. Jan. 1956 [U]).

We found the var. *pictum* Engl., characterized by its red-spotted leaves, grown in pots in a garden at Coronie, Friendship.

2. *Caladium humboldtii* Schott in Oest. Bot. Wochenbl. (1854), p. 417; Schott, Syn. Aroid. (1856), p. 54; Schott, Prod. Syst. Aroid.

(1860), p. 174; Engler in Mart., Fl. Bras. III. 2 (1878), p. 187; Engler in DC., Mon. Phan. Prod. II (1879), p. 467; Engler u. Krause, in Das Pflanzenreich IV 23E (1920), p. 38; — *Caladium argyrites* Lem. in Ill. Hortic. V (1858), t. 185 f. 3; Van Houtte in Fl. d. Serr. 2. Sér. III (1860), p. 104 & t. 1345; Stahel, Nutt. Pl. Sur. 2nd Ed. in Bull. Landbouwproefst. Sur. No. 59 (1944), p. 180; — *Caladium lilliputiense* Rodrig. in Ill. Hortic. XLII (1895), p. 363 & t. 47.

Small plants, up to 22 cm high. Petioles up to 21.5 cm long; basal part vaginate, up to 4 cm long and 0.3 cm wide. Leaf blade 4–10 cm long and 2–5.5 cm wide, peltate, cordate, slightly hastate, white, green-streaked along the white midrib and principal veins. Flowers unknown.

Distribution: Amazonian Brazil, Venezuela; also cultivated.

Coronie, Totness, cultivated (Jonker 559, ster. Feb. 1956 [U]).

3. *Caladium bicolor* (Ait.) Vent. After studying the Suriname material in the field we uphold our opinion expressed in our previous publication (Jonker and Jonker, 1953, l.c.) that the varieties, established by Engler and Krause, are of little value.

We describe, however, a new forma, twice collected by us and, in sterile state, also collected before, by Stahel. The new form is characterized by its large dimensions: 6–8 dm high.

Caladium bicolor (Ait.) Vent. f. **robustum** Jonk. et Jonk., **nov. form.**

Herba valida, 6–8 dm alta. Lamina 35–51 cm longa, 15–30 cm lata. Petiolus ad 87 cm longus. Pedunculus ad 57 cm longus.

Typus: A. M. E. Jonker–Verhoef & F. P. Jonker 459, in herbario U – Surinamo, fluv. Wayombo, in pago Donderskamp.

Distribution: Endemic.

Paramaribo, Coppenamestraat (Jonker 194, fl. Dec. 1955 [U]); Wayombo Riv., Donderskamp (Jonker 459, type, fl. Jan. 1956 [U]); without locality (Stahel s.n., ster. Jan. 1921 [U]).

Colocasia Schott

Colocasia esculenta (L.) Schott is a subspontaneous weed in Suriname and found everywhere in cultivated areas. A small number of cultivars are grown for the tubers and as leafy vegetables. The species very rarely flowers in Suriname. The cultivar "Chinese tajer" is characterized by the light-coloured, greyish-green, slightly pruinose leaves provided with a white spot above, opposite the insertion of the petiole. Petiole and veins white.

Paramaribo, Tourtonnelaan, probably escaped from cultivation (Jonker 682, ster. March 1956 [U]).

Another cultivar: "dasitajer", "dasjitaja", "dasini", or "dasheen" (meaning: from China) is characterized by darker, bluish-green leaves with white veins and provided with a red spot opposite the insertion of the petiole. The latter is purplish-red; the sheath is purple outside and white with red, reticulate venation inside. "Wild" specimens of this cultivar, which are very common e.g. in Paramaribo and often reach a height of over 2 m, are also known as "krastajer" indicating that the plants are too acrid for human food. We collected a single flowering specimen in a garden at Berg en Dal, Suriname Riv. Dr. Lindeman collected a deflorated specimen in a garden at Paramaribo, brought there by Dr. Geijskes from a village at the Tapanahony River.

Peduncle terete, 10–24 cm long. Spathe yellowish-green outside, linear-lanceolate, elongate, ca. 25 cm long and 1.5 cm in diameter, enclosing the much shorter, sessile spadix. Basal, female part of spadix ca. 3 cm long and 8 mm in diameter, covered with 4- to 6–angled, depressed, 1–locular ovaries with 5 (4–6) parietal placentas and crowned by a sessile, much smaller, 5–(4–6)lobed stigma. Ovaries 1.7 mm high and 1 × 2 mm in diameter; between the ovaries numerous scattered pistillodes. Sterile part ca. 2 cm long and 3 mm in diameter, bearing in the basal part pistillodes and in the apical part synandrodia; the latter 0.8 mm high and 2.5 × 0.7 mm in diameter. Male part 4 cm long and 0.5 cm in diameter. Synandria prismatic, truncate, 3- to 6–lobed, consisting of 3–6 stamens; the latter ca. 1 mm long and 1 mm wide. Sterile, apical appendix of the spadix ca. 5 mm long and 3 mm in diameter.

Paramaribo, in garden (Lindeman 3510, defl. Apr. 1953 [U]); id., Tourtonnelaan (Jonker 683, ster. March [U]); Suriname Riv., Berg en Dal, in garden (Jonker 639, fl. Feb. [U]).

The cultivars occurring in Suriname do not agree with the varieties mentioned by Engler and Krause in Das Pflanzenreich IV 23E (1920), p. 65–68.

Alocasia Neck.

Robust herbs provided with an underground rhizome and, sometimes, with a short stem. Petioles rather long, vaginate in the basal part. Leaf blades ovate, cordate or peltate. Plants usually with several inflorescences. Spathes large, coloured. Spadices consisting from the base upwards of a female part, a short sterile part, a male part and a long, sterile appendix. Ovaries usually 1-locular with 3–4 parietal placentes each with two basal ovules.

Distribution: Tropical Asia, New Guinea included. A number of species introduced in other tropical countries.

1. *Alocasia indica* (Roxb.) Schott in Oest. Bot. Wochenbl. IV (1854), p. 410; Schott, Syn. Aroid. (1856), p. 46; Schott, Prodr. Syst. Aroid. (1860), p. 144; Engler in DC., Mon. Phan. Prod. II (1879), p. 501; Engler u. Krause in Das Pflanzenreich IV 23E (1920), p. 87; — *Arum indicum* Roxb., Fl. Ind. III (1832), p. 498.

Stout plant, usually ca. 1–2 m high, rosulate or, in older specimens, provided with a thick, fleshy stem. Leaf blade pergamentaceous, ovate, rounded and mucronate at the apex, cordate at the base, up to 76 cm long and 50 cm wide. Petiole thick, fleshy, up to 140 cm long and 4 cm in diameter, vaginate in its lower half; sheath up to 8 cm wide. Cataphylls pergamentaceous, lanceolate, acute, up to 35 cm long and 4–5 cm wide. Peduncle terete, up to 54 cm long. Spathe up to 23 cm long; basal part tubular, ovoid, coriaceous, up to 5 cm long; limb spreading, broadly elliptical, rounded and mucronate to shortly cuspidate at the apex, up to 18 cm long and 6.5 cm wide. Spadix shorter than the spathe, basal part enclosed by the tube and base of the spathe limb; upper part patent from the spathe. Female part 1.8 cm long and 0.7 cm in diameter; ovaries obconical, 1-locular with 3 parietal placentas each with two basal ovules, ca. 2 mm high and 1.5 mm in diameter, crowned by the small, sessile, 3-lobed stigma. Sterile part, between the female part and the male part, constricted in the middle, 1.4 cm long and 0.6 cm in diameter. Male part ca. 2.6 cm long and 0.9 cm in diameter; synandria consisting of 4–6 stamens, 2 mm high and 1.5 mm in diameter. Appendix up to 12 cm long, clavate, acute or obtuse, covered with a dense mass of small synandrodia, variable in shape and size.

Distribution: tropical Asia, introduced in other tropical countries.

var. *metallica* (Schott) Schott, Prod. Syst. Aroid. (1860), p. 415; Engler in DC., Mon. Phan. Prod. II (1879), p. 502; Engler u. Krause in Das Pflanzenreich IV 23E (1920), p. 88; Birdsey, The cult. Aroids (1951), p. 138; — *Alocasia metallica* Schott in Oest. Bot. Wochenbl. IV (1854), p. 410; Schott, Syn. Aroid. (1856), p. 46; non *Alocasia metallica* W. J. Hook. in Bot. Mag. (1860), t. 5190; — *Caladium metallicum* Hort., Van Houtte, Fl. d. Serr. 2. Sér. III (1860), p. 115; — *Caladium plumbeum* C. Koch and *Xanthosoma plumbeum* C. Koch in Berl. Allg. Gartenztg. XVII (1857), p. 136; — *Alocasia plumbea* (C. Koch) Van Houtte in Fl. d. Serr. 2. Sér. XXI (1875), p. 93, t. 2206.

Petiole and lower surface of the leaf blade blackish purple; upper surface shining, purplish green. Leaf sheath cream-coloured to pink inside. Cataphylls pink. Peduncle light purple. Tubular part of the spathe dark brownish purple; limb greenish with purple stripes to pink outside, yellowish green or white to pink inside. Flowers weakly fragrant. Female part of the spadix light yellow; sterile part light yellow; male part white to creamy; appendix light yellow to cream-coloured.

Distribution: Java, Borneo; introduced to other tropical countries: in gardens in S. Florida and tropical America, sometimes escaped. In Suriname richly flowering.

Commewijne Riv., Margrita (Jonker 342, fl. Jan. 1956 [U]); Paramaribo, Tourtonnelaan (Jonker 477, fl. Jan. 1956 [U]; Jonker 679, fl. March 1956 [U]).

Vernacular names: Zwarte tajer, Indiaanse tajer, Blakka taja.

2. *Alocasia macrorrhiza* (L.) Schott in Oest. Bot. Wochenbl. IV (1854), p. 409; Schott, Syn. Aroid. (1856), p. 45; Schott, Gen. Aroid. (1858), t. 40; Schott, Prod. Syst. Aroid. (1860), p. 146; Engler in Mart., Fl. Bras. III. 2 (1878), p. 202; Engler in DC., Mon. Phan. Prod. II (1879), p. 502; Engler u. Krause in Das Pflanzenreich IV 23E (1920), p. 84, Fig. 15; Birdsey, The cult. Aroids (1951), p. 24; — *Arum macrorrhizum* L., Spec. Plant. (1753), p. 965; — *Arum peregrinum* L., Spec. Plant. (1753), p. 966; Plumier, Pl. Amer. (1755), p. 25, t. 36; Aubl., Pl. Guian. Fr. II (1775), p. 835; — *Colocasia macrorrhiza* (L.) Schott, Melet. I (1832), p. 18; — *Colocasia peregrina* (L.) Schott, Syn. Aroid. (1856), p. 42.

Large, rosulate herbs, up to 5 m high, sometimes provided with an aerial stem when older. Rhizome tuberous, edible. Petioles vaginate in the basal half, ca. 136 cm long, thick, swollen; sheath ca. 6 cm in diameter. Leaf blade ovate, coriaceous, erect, ca. 70 cm long and 45 cm wide, acute and shortly cuspidate at the apex, cordate at the base. Lower surface light green and provided with prominent, yellow veins. Margin sinuate. Basal lobes ovate, obtuse. Sinus triangular, not penetrating to the main ribs of the basal lobes; the two main ribs about rectangular to each other.

Distribution: a native of tropical Asia, cultivated and subspontaneous in other tropical countries. Never observed in flowering state in Suriname. In 1737 Linnaeus already mentioned, in his Hortus Cliffortianus, this species from America. Aublet recorded it, in 1775, from French Guiana. The culture of this species has apparently disappeared in Suriname.

Near Paramaribo, road to Leonsberg, in abandoned plantation (Jonker 519, ster. Feb. 1956 [U]); Lower Suriname Riv., plant. Dordrecht (Lindeman 5764, ster. Apr. 1955 [U]).

Vernacular names: loemboe (Jav.), krassietaja, krastajer.

cultivar *variegata* Hort.

Leaves yellow-variegated.

Cultivated in gardens, Paramaribo.

Typhonium Schott

Small, rosulate, stemless herbs. Underground part tuberous. Leaves petiolate, sagittate to 3-lobed or 3-partite or pinnatisect. Peduncle short. Spathe convolute in the basal part; limb spreading, rather large, acuminate. Spadix consisting of a basal, female part covered with naked, 1-locular ovaries containing 1 or 2 basal ovules, a sterile part covered with staminodes or partly naked, a male part densely covered with naked flowers consisting of two stamens, and a sterile, stipitate, exserted, apical appendix.

Mrs. E. Geijskes–Sollewijn Gelpke drew our attention to a small Aroid growing as a weed in the streets of the centre of Paramaribo, especially in the vicinity of the Governor's House. We collected a specimen flowering in her garden. It appeared to belong to the Asiatic species *Typhonium trilobatum* (L.) Schott recorded by Simmonds from Trinidad as naturalized in that island. According to Engler in Das Pflanzenreich IV 23F (1920), p. 115, this is *T. divaricatum* (L.) Dcne. Linnaeus, however, based his *Arum divaricatum* on the good illustration of "*Nelenschena major*" by Rhede, Hort. Mal. XI (1692), p. 39, t. 20. This species is characterized by the staminodes. The part of the spadix between the male part and the female part is covered over its whole length with patent staminodes of which those on the basal half are clavate and those on the upper half vermiform. Synonyms are *Arum cuspidatum* Bl. in Cat. Hort. Buitenzorg, p. 101 and *Typhonium cuspidatum* (Bl.) Bl., Rumphia I (1835), p. 133, t. 30. Also belonging to this species is the drawing of *Arum flagelliforme* Roxb. in Wight's Icon. III (1844), p. 6, t. 791. *Arum flagelliforme* Lodd., Bot. Cab. IV (1823), t. 396 too belongs in the synonymy and consequently also *Typhonium flagelliforme* (Lodd.) Bl., Rumphia I (1835), p. 134, figured by Engler in Das Pflanzenreich l.c., p. 113, Fig. 16.

Typhonium trilobatum (L.) Schott is characterized by a naked part of the spadix, between the female and the male part, with only basal whorls of acute, orange, erect staminodes. Linnaeus based his species on Ray, Hist. Plant. III (1704), p. 575, no. 17; on Hermann, Par. Bat. (1705), p. 78, t. 78; and on Commelin, Hort. Med. Amstel. (1697), p. 97, fig. 51. Illustrations of this species are to be found in Miller, Fig. Plant. Gard. Dict. I (1760), Pl. 52, fig. 2; Curtis, Bot. Mag. (1796), t. 339; and a detailed one in Curtis, Bot. Mag. (1822), t. 2324. Ray and Hermann, however, mentioned as a synonym *Nelenschena major* Rhede. But as Linnaeus himself only mentioned the latter in the synonymy of *Arum divaricatum*, we follow him in this.

Typhonium roxburghii Schott is also often confused with the two above mentioned species. It is characterized too by the sterile part of the spadix which is provided with basal whorls of hanging, uniform staminodes.

Typhonium trilobatum (L.) Schott, Wiener Ztschr. III (1829), p. 72; Schott, Aroid. I, 1853 (1855), p. 11, t. 16; Schott, Syn. Aroid. (1856), p. 18; Schott, Prod. Syst. Aroid. (1860), p. 108; Simmonds in Kew Bull. 1950 (1951), p. 405; — *Arum trilobatum* L., Spec. Plant. (1753), p. 965; Curtis, Bot. Mag. (1796), t. 339; — *Arum divaricatum*, non L., Wight, Icon. Pl. Ind. Or. III (1844), p. 76, t. 790; — *Typhonium divaricatum* auct., non Dcne, Blume, Rumphia I (1835), p. 130, t. 36; Schott, Aroid. I, 1853 (1855), p. 12, t. 18; Engler in DC., Mon. Phan. Prod. II (1879), p. 611; Engler in Das Pflanzenreich IV 23F (1920), p. 115; — *Arum trilobatum β auriculatum* Curtis, Bot. Mag. (1822), t. 2324; — *Arum acaule foliis trilobus, flore sessile radicato* Linn, Flor. Zeylan. (1748), n. 326, p. 155.

Tuber subglobose, ca. 2 cm in diameter. Petiole up to 12.5 cm long, the basal 3 cm vaginate; sheath white along its margin. Apical part of the petiole semiterete, slightly sulcate. Leaf blade herbaceous, ovate, hastate, acuminate, up to 9 cm long and up to 6.5 cm wide at the base; basal lobes triangular, obtuse, 3.5–4.5 cm long and up to 2 cm wide; both halves of the sinus rounded, penetrating to the main ribs of the basal lobes; naked part of the main ribs ca. 0.5 cm long. Peduncle up to 3 cm long. Inflorescence producing an acrid carrion smell, flowering during a single day only. Basal part of the spathe tubular, ca. 1.5 cm long and 1 cm in diameter, green. Limb triangular, ovate, long-cuspidate, brownish-purple inside with a velvety sheen, becoming greenish towards the base and brownish-green outside, ca. 14 cm long and up to 5 cm wide; cusp contorted, especially when older or in dried state, ca. 7 cm long. Spadix sessile. Female part 2.5 mm long, included in the tubular part of the spathe, covered with light-yellowish-green, 1.5 mm high ovaries; the latter crowned with a small, disciform stigma beset with minute, dark red glands. Sterile part also included, 1.2 cm long, naked for the upper 6 mm; basal half bearing spirally arranged, subulate, erect, orange, 4 mm long staminodes. Male part 5–6 mm long and 3.5 mm in diameter, enclosed by the basal part of the limb, densely covered with orange flowers. Appendix shortly stipitate, subulate, brownish-purple, ca. 12.5 cm long and up to 3 mm in diameter, obliquely truncate at the base; stipe up to 2 mm long.

Distribution: Tropical Asia, subspontaneous in Trinidad and Suriname (Paramaribo).

Paramaribo (Jonker 94, fl. Dec. 1955 [U]).

Philodendron Schott

A number of rare species was recollected:

1. *Philodendron fragrantissimum* (Hook.) Kunth. We can now add the following characteristics to the description in Fl. of Sur.:

Liana, provided with hanging aerial roots. Leaf blade coriaceous. Peduncle pinkish, towards its apex white. Spadix subsessile or shortly stipitate; stipe red. Female part of the spadix light yellow; male part white.

Wayombo Riv., Donderskamp, path from river to village (Jonker 461, fl. Jan. 1956 [U]).

Vernacular name: Akĕkwà (Arow.).

2. *Philodendron jenmanii* Krause. Second collection:

Swamp between Lelydorp and Uitkijk (Jonker 311, fl. Dec. 1955 [U]).

3. *Philodendron dioscoreoides* Gleas. Only known, in sterile state, from British Guiana and one collection from Suriname, upper Nickerie River. We visited the upper Nickerie area and observed that the species was rather common there, but always sterile. Palm-stone collectors in that region knew it by the vernacular name IJzerblad (= iron leaf) and stated that it never flowered.

Upper Nickerie Riv., right bank, camp Powiesi Boutoe (Jonker 405, ster. Jan. 1956 [U]).

4. *Philodendron guttiferum* Kunth var. *guttiferum*. Second collection:

Suriname Riv., Brokopondo (Jonker 633, fl. Feb. 1956 [U]).

var. *rudgeanum* (Schott) Jonk. et Jonk. Fourth collection:

Perica Riv., Capoerica ridge (Lindeman 5337, fl. Jan. 1954 [U]).

We have the impression that var. *guttiferum* occurs in the interior and var. *rudgeanum* in the coastal region.

5. *Philodendron sphalerum* Schott. This endemic species was collected for the third time. The following characteristics can be added to the description in Fl. of Sur.: Spathe light green outside, inside creamy white. Spadix creamy white.

Perica Riv., Capoerica ridge (Lindeman 5139, fl. Dec. 1953 [U]).

6. *Philodendron splitgerberi* Schott. The type material, sterile, collected by Splitgerber, has been lost. The original drawings by Schott, however, have been kept in the Vienna herbarium. We collected the species in fertile state.

Philodendron splitgerberi Schott, Prod. Syst. Aroid. (1860), p. 251; Engler in DC., Mon. Phan. Prod. II (1879), p. 376; id. in Engl., Bot. Jahrb. XXVI (1899), p. 524; Krause in Das Pflanzenreich IV 23 Db (1913), p. 44; Jonker and Jonker in Act. Bot. Neerl. II (1953),

p. 358, also published as Med. Bot. Mus. en Herb. Utr. n. 118; Jonker and Jonker in Fl. Sur. I. 2 (1953), p. 60.

Epiphytic climber provided with an apical rosette. Internodes 3–3.5 cm long and 0.6 cm in diameter. Cataphylls decaying to a dense mass of brown fibres. Leaves petiolate, glabrous. Petioles broadly and, at the apex, crisply winged, up to 32 cm long and 1.5 cm wide; those of the rosulate leaves shortly vaginate in the basal 2.5 cm; sheath of the stem leaves up to 10 cm long and 1.5 cm wide, auriculate at the apex. Leaf blade coriaceous, triangular ovate, truncate at the base, acuminate and mucronate at the apex, 26–32 cm long and 10–18 cm wide at the base. Peduncle 5–6 cm long and 0.6 cm in diameter. Spathe closely convolute, 8–10.5 cm long, enclosing the spadix. Basal half swollen, bright red; apical half cream-coloured. Spadix obliquely sessile. Female part 3 cm long and 1.8 cm in diameter; ovaries ca. 7 mm high and 4 mm in diameter, 7–locular; ovules several, biseriate. Sterile part ca. 1 cm long and 0.7 cm in diameter. Fertile male part 5.2 cm long and 0.7 cm in diameter. Male flowers consisting of 3–4 stamens, each of them ca. 1 mm long and 0.7 mm wide.

Distribution: Endemic.

Suriname Riv., 12 km SE of Jodensavanne, camp VIII of Forestry Service (Jonker 648, fl. Feb. [U]).

The following species are new for Suriname:

7. *Philodendron longepetiolatum* Engl., hitherto known from British and French Guiana only and cited in Fl. of Sur. as to be expected. The following characters are to be added to that description:

Leaf blade acute or truncate and often more or less cuneate at the base. Spathe outside bright green on the back and light yellow along the margins, inside creamy yellow. Female part of the spadix light green; male part white.

Suriname Riv., Mapane creek, Suhoza (Lindeman 6720, fl. Dec. 1954 [U]). Note: we also observed the species in flowering state near Kwakoegron, Saramacca Riv. It was, however, impossible to collect it.

8. *Philodendron jacquinii* Schott, Syn. Aroid. (1856), p. 90; Schott, Prod. Syst. Aroid. (1860), p. 259; — *Arum hederaceum* Jacq., Stirp. Amer. (1763), p. 240, t. 152; Willd., Spec. Plant. IV (1805), p. 486, p.p.; — *Philodendron hederaceum* auct., Kunth, Enum. Plant. III (1841), p. 49, p.p.; — *Philodendron hoffmannii* Schott in Oest. Bot. Ztschr. VIII (1858), p. 178; Schott, Prod. Syst. Aroid. (1860), p. 256; Ørst., Praecurs. Fl. Centroam. (1873), p. 59; Engler in DC., Mon. Phan. Prod. II (1879), p. 399; Engler in Engl., Bot. Jahrb. XXVI (1899), p. 553; Krause in Das Pflanzenreich IV 23 Db (1913), p. 125.

Non-rosulate epiphytic climber. Stems, peduncles and petioles often provided with bladders in dried state. Internodes 5–7 cm long and ca. 1 cm in diameter, shortly setose. Leaves petiolate. Petioles shortly setose, up to 23 cm long; the basal 6.5–14 cm vaginate; sheath up to 3 cm wide. Leaf blade papyraceous, ovate, cordate at the base, acute to shortly acuminate and mucronate at the apex, 14–23 cm long and

11–15.5 cm wide; midrib and principal veins shortly setose beneath; basal lobes orbicular, 5–8 cm in diameter; sinus rounded, penetrating to the main ribs of the basal lobes; denudate part of the main ribs up to 1.5 cm long. Peduncle glabrous, 3–6 cm long. Spathe closely convolute, 8–10 cm long and 9 cm wide, green outside, inside red in the basal part and green towards the apex. Spadix sessile, ca. 8 cm long, covered with an evil-smelling slime which attracts insects. Female part up to 2.5 cm long and 1.5 cm in diameter, green; ovaries elongate, prominent, 6 mm high and 2 mm in diameter, 3-locular; each locule containing two basal ovules. Sterile part up to 3 cm long and 0.8 cm in diameter, ivory-coloured. Male part up to 4 cm long and 0.9 cm in diameter, light green to ivory, in dried state sometimes red; male flower consisting of 3 anthers which are 2.5 mm long and 1 mm wide.

Distribution: Central America.

Near Paramaribo, road to Leonsberg, abandoned plantation, epiphyte on *Pimenta officinalis* (Jonker 521, fl. Feb. 1956 [U]).

9. *Philodendron ornatum* Schott. In citing the species by this name, we are uniting *Philodendron rubens* Schott (1856) and *P. tobagense* Engl. (1899) — already united by Simmonds in Kew Bull. 1950 — with *P. ornatum* Schott (1853) and *P. asperatum* (Koch) Koch (1855), based on *Zantedeschia asperata* C. Koch (1853). In accordance with art. 57 of the Int. Code of Botanical Nomenclature (1956) we choose *P. ornatum* Schott (1853). The only difference between *P. rubens* (= *P. tobagense*) and *P. ornatum* (= *P. asperatum*) is the colour of the spathe: red inside in the former and white inside in the latter. In our opinion this is of no specific value.

Philodendron ornatum Schott in Oest. Bot. Wochenbl. III (1853), p. 378; Schott, Syn. Aroid. (1856), p. 84; Schott, Prod. Syst. Aroid. (1860), p. 247; Engler in Mart., Fl. Bras. III. 2 (1878), p. 155; Engler in DC., Mon. Phan. Prod. II (1879), p. 382; Engler in Engl., Bot. Jahrb. XXVI (1899), p. 525; Krause in Das Pflanzenreich IV 23Db (1913), p. 51; — *Zantedeschia asperata* C. Koch, Ind. Sem. Hort. Berol. (1853) App. p. 5; — *Philodendron asperatum* (Koch) Koch, Ind. Sem. Hort. Berol. (1855) App. p. 4; Schott, Syn. Aroid. (1856), p. 85; Schott, Prod. Syst. Aroid. (1860), p. 248; Ender, Ind. Aroid. (1864), p. 85; Engler in Mart., Fl. Bras. III. 2 (1878), p. 156; Engler in DC., Mon. Phan. Prod. II (1879), p. 383; Engler in Engl., Bot. Jahrb. XXVI (1899), p. 525; Krause in Das Pflanzenreich IV 23Db (1913), p. 51; — *Philodendron rubens* Schott, Syn. Aroid. (1856), p. 84; Schott, Prod. Syst. Aroid. (1860), p. 245; J. D. Hooker in Bot. Mag. (1873), t. 6021; Engler in DC., Mon. Phan. Prod. II (1879), p. 389; Engler in Engl., Bot. Jahrb. XXVI (1899), p. 530; Krause in Das Pflanzenreich IV 23 Db (1913), p. 61; Simmonds in Kew Bull. 1950 (1951), p. 402; — *Philodendron imperiale* Schott in Oest. Bot. Ztschr. XV (1865), p. 71; Schott in Peyritsch, Aroid. Maxim. (1879), p. 51, t. 40–42; — *Philodendron tobagense* Engl. in Engl., Bot. Jahrb. XXVI (1899), p. 524; Krause in Das Pflanzenreich IV 23 Db (1913), p. 52.

Climber. Internodes ca. 7.5 cm long and 0.7 cm in diameter.

Cataphylls pink, large, papyraceous, acute, up to 22 cm long and 6 cm wide, 2-crested on the back, decaying to brown fibres. Leaves petiolate. Petiole of the stem leaves consisting of a 9–10 cm long and 1.2 cm wide sheath, which is auriculate at the apex, and a 4 cm long verrucose pulvinus; warts white. Petiole of the rosulate leaves without sheath, 22–33 cm long, white-verrucose towards the leaf blade, especially on the 3.5–5.5 cm long, often pink pulvinus. Leaf blade of the stem leaves triangular-ovate, truncate at the base, cuspidate at the apex, up to 17.5 cm long and 10 cm wide at the base, pink when young; cusp up to 1.5 cm long. Leaf blad of the rosulate leaves ovate, cordate at the base, cuspidate at the apex, up to 48 cm long and 26.5 cm wide. Sinus broadly triangular to rounded and then penetrating to the main ribs of the orbicular basal lobes; denudate part of the ribs 2–2.5 cm long. Basal lobes up to 13 cm in diameter.

Distribution: S. Brazil, Venezuela, Trinidad, Tobago.

Cottica Riv., Moengo, forest near bauxite mines (Jonker 484, ster. Jan. 1956 [U]).

10. *Philodendron hederaceum* Schott, Melet. I (1832), p. 19; Kunth, Enum. Plant. III (1841), p. 49 p.p.; Schott, Syn. Aroid. (1856), p. 90; Schott, Prod. Syst. Aroid. (1860), p. 255; — *Colocasia hederacea sterilis minor folia cordata* Plumier, Descr. Pl. Amer. (1693), p. 39, t. 51 & 55; — *Arum hederaceum* Willd., Spec. Plant. IV (1805), p. 486 p.p.; — *Philodendron scandens* Koch et Sello in Ind. sem. hort. Berol. (1853) App. p. 4; Schott, Syn. Aroid. (1856), p. 83; Schott, Prod. Syst. Aroid. (1860), p. 243; Engler in Engl., Bot. Jahrb. XXVI (1899), p. 528; Urb., Symb. Ant. IV (1903), p. 134; Krause in Das Pflanzenreich IV 23 Db (1913), p. 56; Simmonds in Kew Bull. 1950 (1951), p. 404; — *Philodendron oxycardium* Schott, Syn. Aroid. (1856), p. 82; Schott, Prod. Syst. Aroid. (1860), p. 241; Engler in DC., Mon. Phan. Prod. II (1879), p. 386; Engler in Engl., Bot. Jahrb. XXVI (1899), p. 527; Urb., Symb. Ant. IV (1903), p. 134; Krause in Das Pflanzenreich IV 23 Db (1913), p. 56; — *Philodendron isertianum* Schott, Prod. Syst. Aroid. (1860), p. 242.

Climber. Internodes long. Leaves petiolate, not rosulate. Petiole vaginate in the basal half. Leaf blade ovate, cordate at the base, cuspidate at the apex; sinus narrowly triangular, acute, not penetrating to the main ribs of the basal lobes. Peduncle up to 6 cm long and 0.8 cm in diameter. Spathe tube green after flowering. Ovary oblong, 5-locular; ovules several, biseriate.

Distribution: West-Indian Islands, Guatemala, Venezuela.

Perica Riv., Capoerica ridge (Lindeman 5438, defl. Jan. 1954 [U]).

If *P. hederaceum* is considered a nomen confusum, the correct name for this taxon is *P. scandens* C. Koch et Sello.

11. **Philodendron wayombense** Jonk. et Jonk., **nov. spec.** (Fig. 1).

Caudex scandens internodiis ad 15 cm longis, ad 2 cm crassis. Foliorum petiolus teres, 34–57 cm longus, ad 7 cm longitudinis vaginatus. Lamina pergementacea, 54–61 cm longa, 30–60 cm lata, ambitu cordato-ovata, margine inciso sinuata. Pedunculi 1-3 ex

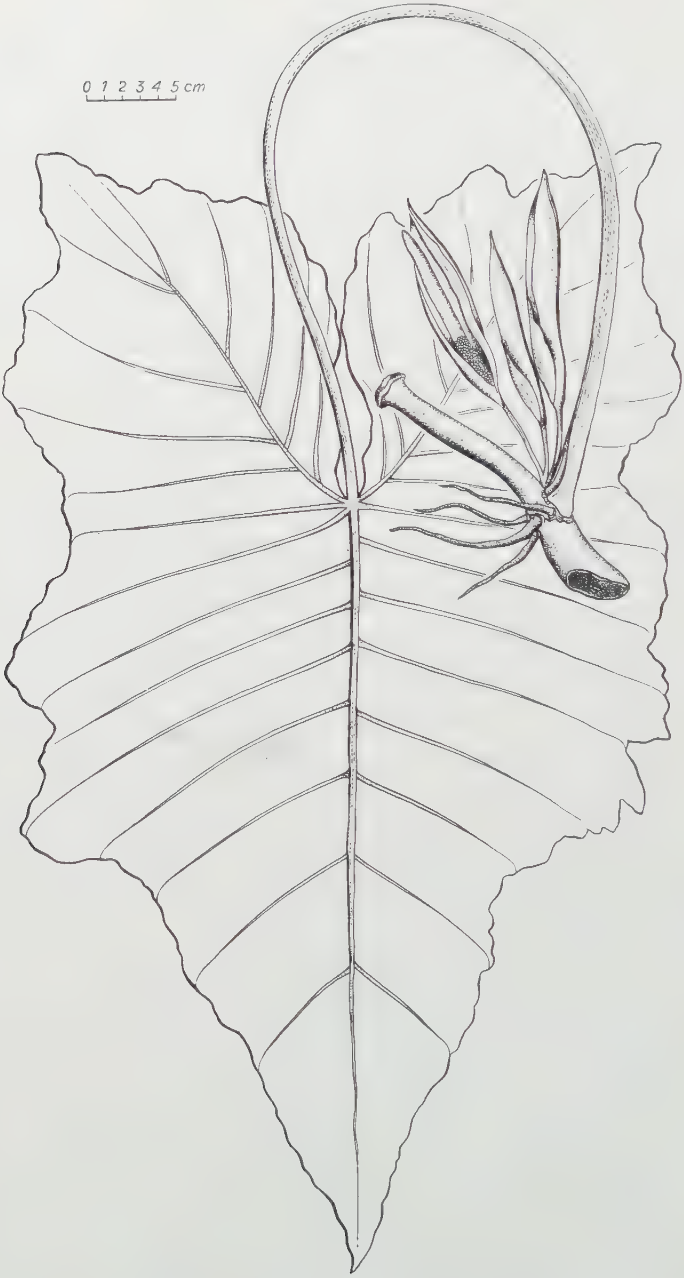

Fig. 1. *Philodendron wayombense* Jonk. et Jonk., typus.

axillo provenientes, 1-8 cm longi. Spatha viridis, rubro-maculata, ca. 14 cm longa, 4 cm lata. Spadix oblique sessilis, pars feminea ad 3.5 cm longa, 0.7 cm crassa, mascula basi sterilis, ad 7 cm longa, 0.7 cm crassa. Pistilla ovoidea, 2 mm longa, 1 mm lata, 5–6-locularia; ovula 5–6 placentae breviae affixa.

Typus: A. M. E. Jonker–Verhoef et F. P. Jonker 462, in herbario U. Surinamo ad flumen Wayombo prope Donderskamp.

The leaves of this new species resemble those of *Philodendron subincisum* Schott from Mexico, erroneously considered by Engler a synonym of *P. lacerum* (Jacq.) Schott. In the leaves of *P. wayombense*, however, the apical lobe is provided with ca. 9 pairs of veins; this number being 6 in *P. subincisum*. Moreover, the leaf blade is ovate in *P. subincisum* and slightly 5-lobed in *P. wayombense*. For this reason the species is related to *P. pedatum* (Hook.) Kunth, of which the first leaves are distinctly 3– to 5–lobed with a large terminal lobe, and the later leaves pinnatifid or pinnatisect. Also the number of locula of the ovary and the number of ovules point to a relationship with the latter species.

The plants contain a milky juice of which the smell strongly resembles that of raw carrots.

Wayombo Riv., Donderskamp, path from river to village (Jonker 462, fl. Jan. 1956 [U]).

Vernacular name: mesji tjoepie (Arow.).

These investigations have been carried out in the Botanical Museum and Herbarium of the State University of Utrecht, Netherlands (Director: Dr. J. Lanjouw) and in the laboratory of the WOSUNA at Paramaribo, Suriname. We wish to tender our most sincere thanks to the foundation "WOSUNA" (Scientific Research Suriname and the Netherl. Antilles) for the opportunity to visit Suriname and to study the Aroids in the field. A special word of thanks is due to Dr. D. C. Geijskes, then director of WOSUNA at Paramaribo, and to his successor Mr. J. Heiting.

The authors wish to express also their thanks to the directors of the Royal Botanic Gardens, Kew (Surrey), England and of the State Herbarium, Leiden, Netherlands, for the loan of herbarium specimens.

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STUDIES ON THE POST-BOREAL VEGETATIONAL HISTORY OF SOUTH-EASTERN DRENTHE (NETHERLANDS)

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INTRODUCTION

In this paper the results of some palynological investigations of peat deposits in south-eastern Drenthe will be discussed. The location of the profiles to be discussed is indicated on the map of Fig. 1. This map, which is a slightly modified copy of the Geological Map (No. 17, sheets 2 and 4; No. 18, 2 and 4), gives a survey of the soils in the Emmen district.

Peat formation took place chiefly in the Hunze *Urstromtal*, which to the west is bordered by the Hondsrug, a chain of low hills. It may be noted that the greater part of the raised bog has now vanished on account of peat cutting. In the eastern part of the Hondsrug fairly fertile boulder clay reaches the surface, whereas more to the west in general the boulder clay is covered by a more or less thick deposit of cover sand. Fluvio-glacial deposits are exposed on the eastern slope of the Hondsrug.

Unfortunately, no natural forest has been left in south-eastern Drenthe. Under present conditions the climax vegetation in areas with boulder clay on or slightly below the surface would be a *Querceto-Carpinetum subatlanticum* which is rich in *Fagus*, that in the cover sand areas—dependent on the depth of the boulder clay—a *Querceto roboris-Betuletum* or a *Fageto-Quercetum petraeae* (*cf.* Tüxen, 1955).

In contrast to the diagrams from Emmen and Zwartemeer previously published (Van Zeist, 1955a, 1955b, 1956b) which provide a survey of the vegetational history of the whole Emmen district, the diagrams from Bargeroosterveld and Nieuw-Dordrecht have a more local character. The latter two profiles are in the border zone of the raised bog, only a short distance from the higher soils of the Hondsrug. In these diagrams the influence of prehistoric man on vegetation comes out better than it does in those from the more central parts of the raised bog.

The profile of Nieuw-Dordrecht was sampled during the excavation of a trackway (Van Zeist, 1956a). This trackway consisted mostly of split tree stems, of a length of about 3 m, which were laid on the peat transversally side by side. A radiocarbon dating of a piece of wood from this trackway gave an age of 1885 ± 55 B.C. (Gro 1087).

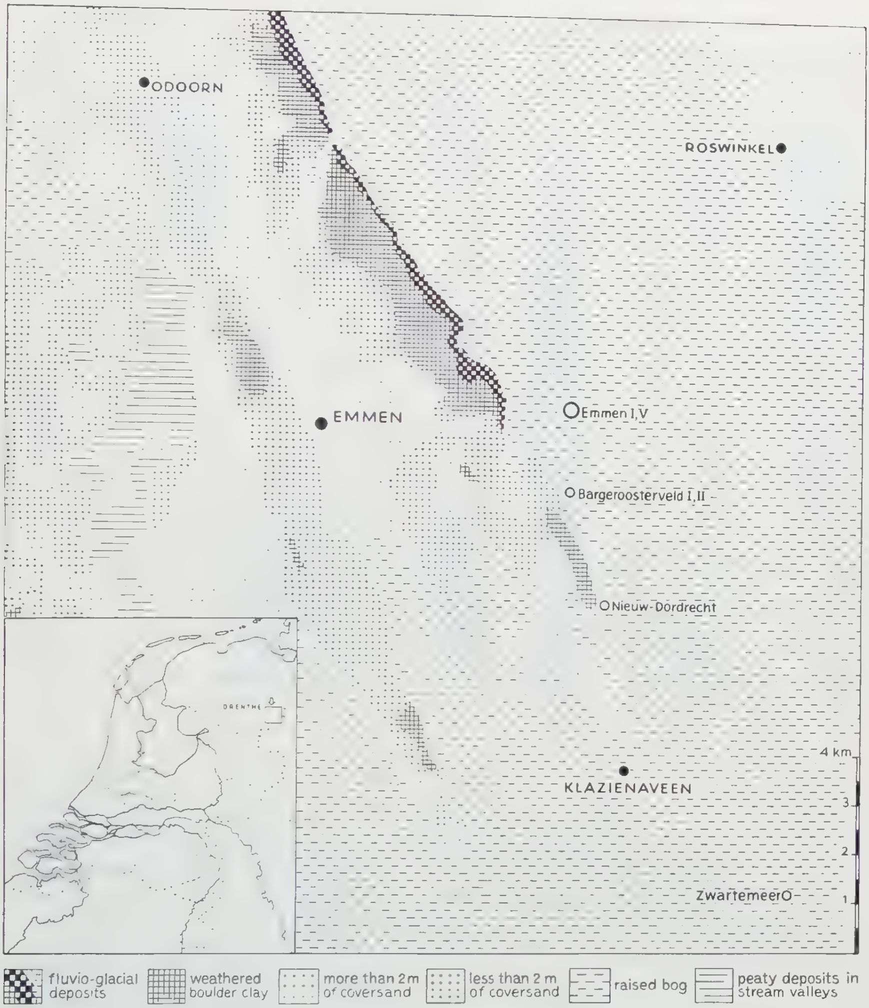

Fig. 1. Soil map of the Emmen region with location of the profiles discussed in this paper.

The samples from the Bargeroosterveld profiles were collected on the occasion of the excavation of the remains of a wooden building placed on the peat. This structure, which was surrounded by a circle of rather small stones, had undoubtedly a ritual purpose (WATERBOLK and VAN ZEIST, in preparation). The level of this building, which according to a radiocarbon measurement is to be dated at 1045 ± 65 B.C. (Gro 1552), is indicated in the Bargeroosterveld II diagram.

A summary of the results previously published gives the simplified diagram Emmen I (VAN ZEIST, 1955a, Fig. 4). The Boreal and early Atlantic part of this diagram has been omitted here (Fig. 2). The

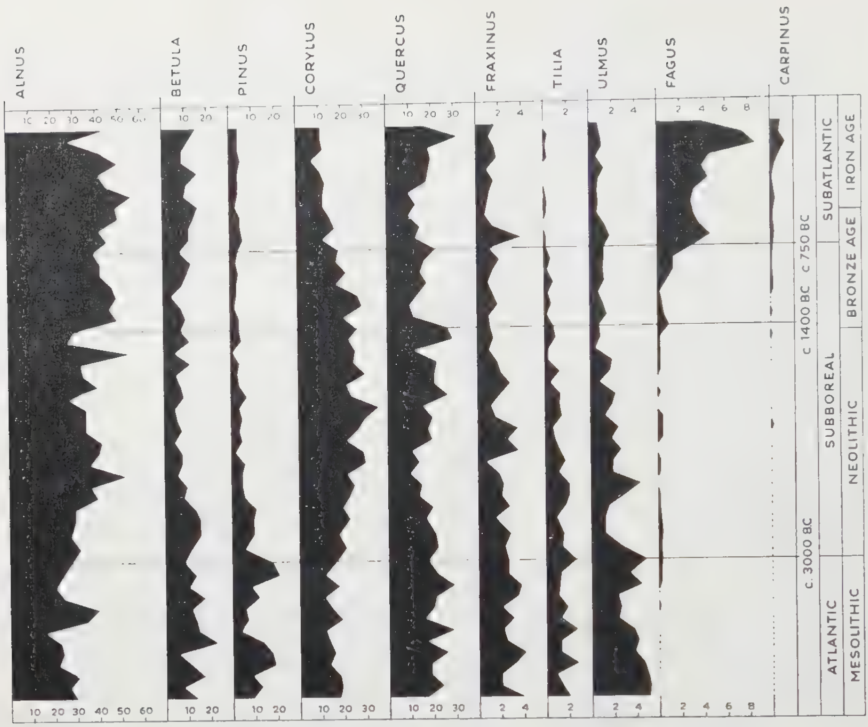

Fig. 2. Simplified Emmen I diagram.

dates on the right side were obtained on the ground of radiocarbon measurements of a series of samples from the same raised bog. Moreover—in order to prevent a possible misunderstanding—the archaeological and palaeobotanical periods have been added to this diagram.

The Atlantic/Subboreal border is placed at the fall of *Ulmus*. From this level on, indications of the activity of Neolithic farmers can be observed in the pollen diagrams from this region. It appeared that the increase of *Fagus* to about 1 % coincides approximately with the transition from the Neolithic to the Bronze Age. The Subboreal/Subatlantic border is placed at the first important increase of *Fagus* (up to about 5 %).

The prehistoric occupation of the Emmen district

As the influence of man on vegetation is to be discussed in this paper, it is necessary to summarize very briefly the prehistoric occupation of this region. The interference of man with the natural vegetation began in the Neolithic with the settling of the first farmers. In the northern Netherlands three Neolithic cultures occurred. The megalithic tombs (*hunebedden*) ,a relatively large number of which are found in the south-eastern part of the Hondsrug, attest the presence of the Funnel Beaker Culture. Pottery of the Bell Beaker and Protruding

Foot Beaker Cultures—both tumulus-burying cultures—is also known from this region (*cf.* VAN DER WAALS and GLASBERGEN, 1955). According to present opinion the Neolithic in the northern Netherlands lasted from about 2500 to about 1500 B.C.

In south-eastern Drenthe a considerable number of bronze objects has been found. From the fact that these objects cover the whole of the Bronze Age (1500–500 B.C.) it can be concluded that during that period this region had continuous habitation (BUTLER, oral communication).

Also from the Iron Age (500 B.C.–400 A.D.) many traces have been left in the Emmen district. In addition to the urnfields, which started already in the second half of the Bronze Age, and some burial mounds, systems of Celtic fields—arable plots—have to be mentioned (*cf.* WIERINGA, 1958, Fig. 5).

THE DIAGRAMS

In order to provide a better impression of the composition of the forest on the higher soils and of the alterations in the vegetation effected by changes of climate or interference of man, the concept "*Quercetum-mixtum sensu lato*" has been introduced in this paper. In this are included *Quercus*, *Tilia*, *Ulmus*, *Fraxinus*, *Fagus*, *Carpinus*, *Acer* and *Taxus*. In the diagrams the pollen frequencies of these trees are shown as percentages of the sum of the "*Quercetum-mixtum s.l.*" Quantitatively important pollen types which are herewith left out of consideration are *Pinus*, *Alnus* and *Betula*. During the Preboreal and Boreal the main trees of the forest on the higher soils were *Betula* and *Pinus*. It was not until the second part of the Boreal and the beginning of the Atlantic that the components of the classical *Quercetum-mixtum*, namely *Quercus*, *Tilia*, *Ulmus* and *Fraxinus*, were able to expand considerably. For the Preboreal and Boreal period the "*Quercetum-mixtum s.l.*" diagrams certainly would not give a correct picture of the forest vegetation. In the first part of the Atlantic the composition of the forest was still liable to continuous alteration in consequence of the gradual increase of the various deciduous trees. It was not until later in Atlantic time that a certain equilibrium in the vegetation was reached.

It is beyond doubt that in the second part of the Atlantic and in the later periods *Pinus* and *Betula* formed part of the vegetation on the poorer soils, although in general their share would not have been very important. After a forest clearing, however, *Betula* would locally have shown a considerable increase of a temporary nature (*cf.* IVERSEN, 1941). It must likewise be taken into account that *Alnus* was present in the wettest parts of the mixed oak forest. That these trees have been left out of the "*Quercetum-mixtum s.l.*" is due to the fact that locally they played an important part in the bog vegetation. Birch, alder and pine were growing on the peat, especially in the border zone and along the streams. One may assume that a great part of the pollen of *Pinus*, *Betula* and *Alnus* in the post-Boreal peat deposits from this region was produced by trees which belonged to the vegetation of the bog. Moreover, *Alnus* would have been common in the stream valleys. For *Ulmus* and *Fraxinus* these peaty valleys would certainly not have formed a suitable environment.

The pollen frequencies of the herbs represented in the diagrams are expressed as percentages of the sum of the components of the "*Quercetum-mixtum s.l.*" It would perhaps have been better to use as the basis of calculation the pollen sum of the "*Quercetum-mixtum s.l.*" and these herbs. This, however, encountered the difficulty that in certain parts of the profiles from Bargeroosterveld and Nieuw-Dordrecht a considerable amount of Gramineous pollen has to be attributed to a local production. Generally no curves are given here for those pollen types which for the greater part would have been produced by plants which formed part of the bog vegetation.

The *Corylus* pollen frequencies are shown as percentages of the sum the "*Quercetum-mixtum s.l.*" and *Corylus*.

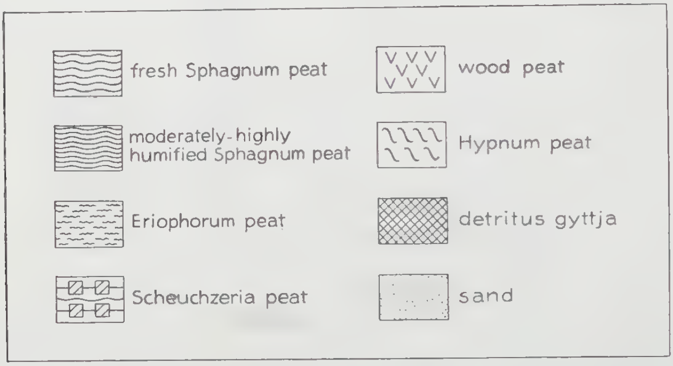

Fig. 3. Key to the symbols employed in the pollen diagrams.

As this manner of representing the results differs from the usual one, new diagrams have been drawn for the profiles from Zwartemeer and Emmen (Figs. 6, 7 and 10). For practical reasons nearly all herbs have been omitted in these diagrams, whereas from the profiles Emmen I and V the lower part, comprising the early Atlantic and older periods, has not been given. From the Bargeroosterveld and Nieuw-Dordrecht profiles also a traditional tree pollen diagram (*Corylus* included in the Σ AP) is published here (Figs. 4, 8 and 12). These diagrams have been simplified in that the components of the "*Quercetum-mixtum s.l.*" have been taken together here.

THE FALL OF ULMUS AND THE FIRST FARMERS

A striking feature in the pollen diagrams from western and north-western Europe is the fall of *Ulmus*. This decline of the *Ulmus* curve is generally accepted as a criterion for defining the border between the Atlantic (zone VII in Denmark and Norway, zone VIIa in England and Ireland, zone VI and VII according to Firbas, 1949) and the Subboreal (zones VIII, VIIb and VIII respectively).

In the diagrams from Denmark published by IVERSEN (1941) the recession of *Ulmus* coincides with an important decrease of *Hedera*. As this behaviour of *Hedera* is ascribed to a deterioration of climate after the post-glacial optimum (IVERSEN, 1941, 1944), it may be supposed that the decrease of *Ulmus* was due to the same factor. Also the circumstance that this phenomenon can be observed in so many diagrams would be in favour of a climatological cause. This the more as a number of radiocarbon datings suggests that in a large area the fall of *Ulmus* was a more or less synchronous phenomenon that can be dated at about 3000 B.C. (see Table I).

However, a climatological explanation for the decrease of *Ulmus* encounters difficulties. In the Danish diagrams *Fraxinus* shows a not unimportant increase simultaneously with the fall of *Ulmus*. For that reason Iversen supposes that it was *Ulmus carpinifolia* which as a consequence of the change in climate disappeared partly or wholly from Denmark. *Ulmus carpinifolia*, whose northern limit lies in Schleswig-Holstein, shows in ecological respect much resemblance with *Fraxinus excelsior*. The latter, however, ranges farther to the north-east, indicating that this tree can bear a more raw climate than *Ulmus carpinifolia*.

A serious drawback in the study on the behaviour of *Ulmus* in prehistoric times is that it has hitherto been impossible to separate the pollen of the various elm species. For that reason the palynological investigation cannot show the share of each *Ulmus* species in the pollen rain.

Concerning Norway, where undoubtedly only *Ulmus glabra* is the elm species in question (*cf.* HAFSTEN, 1956, p. 79), the diagrams from the relatively continental Oslo Fjord area show a descent of *Ulmus* that is also accompanied by an increase of *Fraxinus*. In northern and north-eastern Europe *Ulmus glabra* exceeds the limit of *Fraxinus excelsior*. For that reason it is difficult to imagine that *Fraxinus* would have been able to expand during a deterioration of climate of a nature that could cause a decline of *Ulmus glabra*.

In extremely oceanic western Norway the fall of *Ulmus* is even coupled with an increase of *Tilia* and *Hedera* (FAEGRI, 1940, 1944a, 1944b). In the post-glacial pollen diagrams from Ireland—where probably also only *Ulmus glabra* has to be considered—a marked decrease of *Ulmus* can be observed (MITCHELL, 1951, 1956), although *Hedera* does not show a decline at the same time (GODWIN, 1956, Fig. 50). Also in the Emmen district the fall of *Ulmus* is not attended by a decrease of *Hedera* (*cf.* Fig. 14).

Thus, in the diagrams from various regions one observes a descent of *Ulmus*, but no decrease of *Hedera*. In view of the present distribution of *Ulmus glabra* and *Hedera* it is not likely that a deterioration of climate could cause a recession of this elm species without effecting ivy. Consequently, in the regions, where there can only be a question of *Ulmus glabra*, a climatological factor can hardly be held responsible for the fall in the *Ulmus* curve if there is no decline of *Hedera*.

GODWIN (1956) put forward the suggestion that it could have been

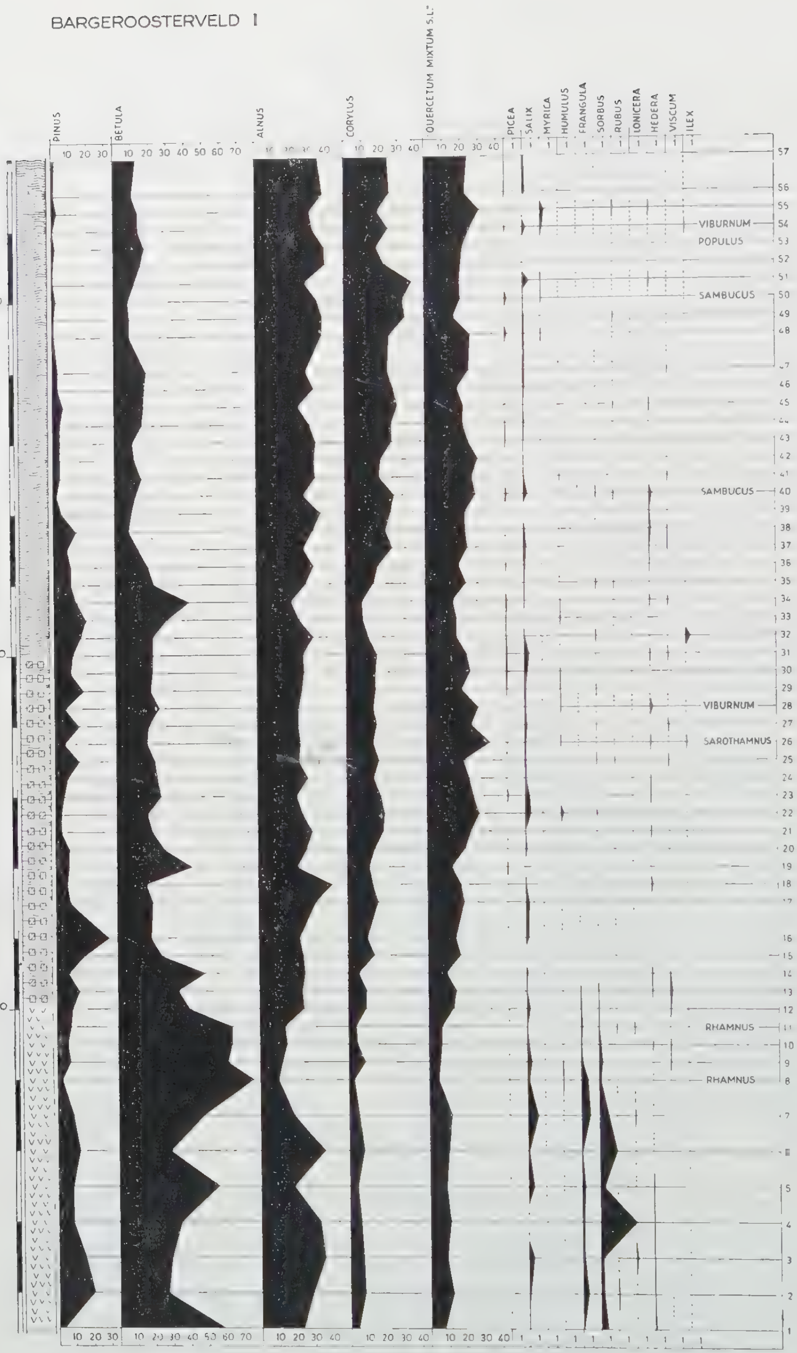
BARGEROOSTERVELD I
PINUS
BETULA
ALNUS
CORYLUS
QUERCETUM MIXTUM S.L.
PICEA
SALIX
MYRICA
HUMULUS
FRANGULA
SORBUS
RUBUS
LONICERA
HEDERA
VISCUM
ILEX
10 20 30
10 20 30 40 50 60 70
10 20 30 40
10 20 30 40
10 20 30 40
150
200
250
VIBURNUM
POPULUS
SAMBUCUS
SAMBUCUS
VIBURNUM
SAROTHAMNUS
RHAMNUS
RHAMNUS
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Fig. 4.

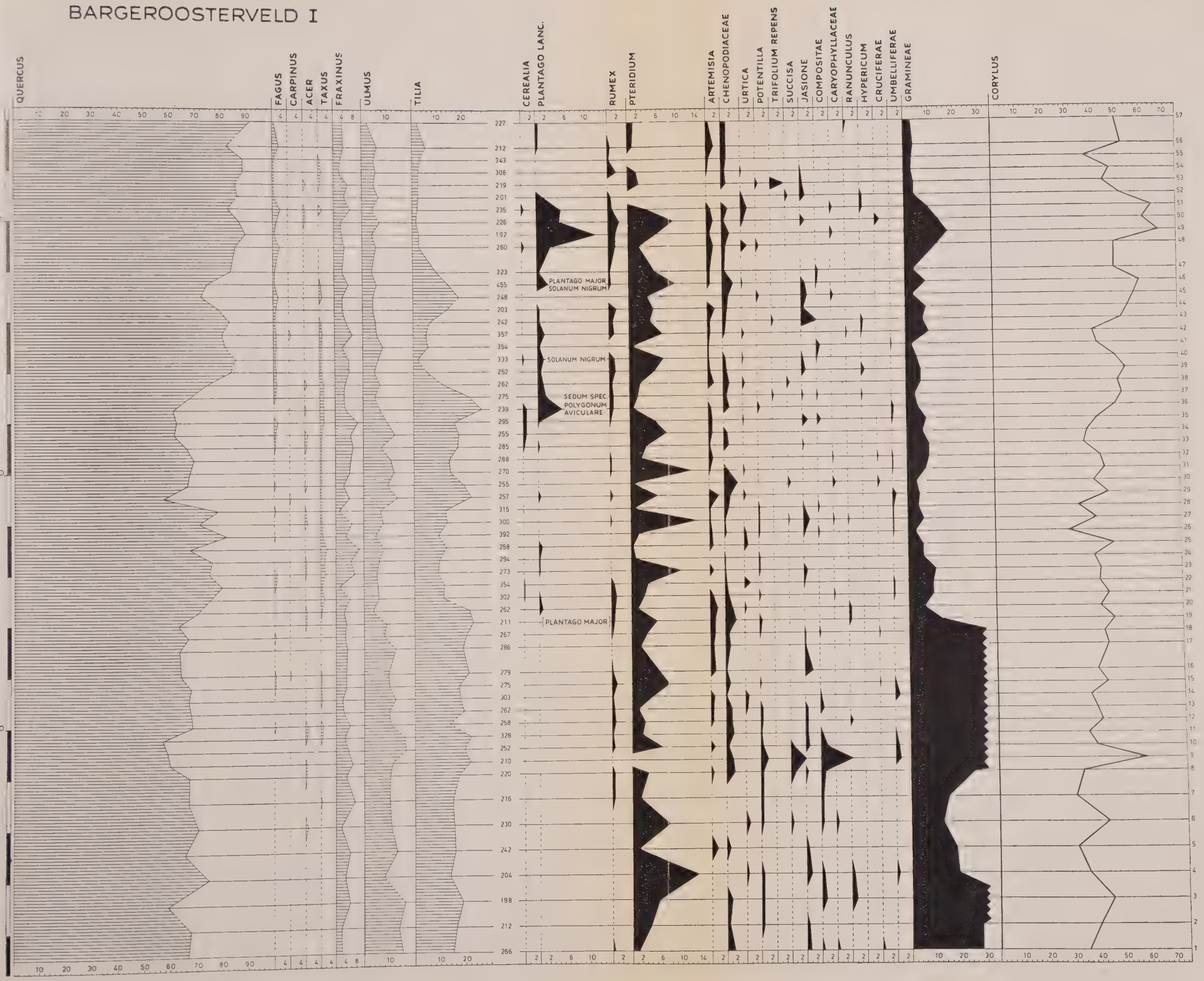
BARGEROOSTERVELD I
QUERCUS
FAGUS
CARPINUS
ACER
TAXUS
FRAXINUS
ULMUS
TILIA
CEREALIA
PLANTAGO LANC.
RUMEX
PTERIDIUM
ARTEMISIA
CHENOPODIACEAE
URTICA
POTENTILLA
TRIFOLIUM REPENS
SUCCISA
JASIONE
COMPOSITAE
CARYOPHYLLACEAE
RANUNCULUS
HYPERICUM
CRUCIFERAE
UMBELLIFERAE
GRAMINEAE
CORYLUS
PLANTAGO MAJOR
SOLANUM NIGRUM
SOLANUM NIGRUM
SEDUM SPEC.
POLYGONUM AVICULARE
PLANTAGO MAJOR
200
250

Fig. 5.

an increase of late spring frost that caused the fall of *Ulmus*. According to this author MELVILLE was able to demonstrate that fruit formation in the British species of elm is very susceptible to late spring frost once the flowers are open. It is *Ulmus glabra*, the latest-flowering British elm, which appears to escape late frost damage most frequently. This, however, cannot have been the factor that caused the fall of *Ulmus* at the beginning of the Subboreal, as at the same time *Fraxinus* —which is also very susceptible to late spring frost—shows an expansion in various areas.

FAEGRI (1944b) has pointed to the effect of the activity of prehistoric man on the production of *Ulmus* pollen. Especially the leafy branches of the elms would have been cut in order to give them to the cattle. Until recently the foliage of various kinds of trees was used as cattle fodder in mountainous regions with a serious shortage of grass. In remote areas, among others in Norway, this custom is still practised (*cf.* VE, 1930; BROCKMANN–JEROSCH, 1918). Heavy pruning of the trees promotes the sprouting of new shoots, which can then be harvested again after some years. BROCKMANN–JEROSCH (1918) reports that the foliage of *Ulmus* and *Fraxinus* is the most suitable for cattle fodder; in second place comes that of *Quercus*, *Acer*, *Tilia* and others. According to this author many kinds of trees can be utilized as cattle fodder. VE (1930) mentions that in Springtime in Norway even the still leafless twigs of the elm were cut in order to serve as food for the cows.

TROELS-SMITH (1953, 1955) carried out extremely detailed palynological investigations of the first farmers both in Switzerland (Michelsberg and Early Cortaillod Culture) and in Denmark (Ertebølle Culture). On the basis of the very low percentages of *Plantago lanceolata* this author arrives at the conclusion that little or no pasture land was available for the cattle. The domestic animals would have been kept in stalls or at least within an enclosure. For feeding the cattle people depended to a high degree on the foliage of various trees. Confirmation of this hypothesis is provided by the results of archaeological investigations in Switzerland. At the excavation of a settlement near Robenhausen, leaves of deciduous trees and twigs of the silver fir, likewise very suitable as cattle fodder, were met with (HEER, 1865, p. 7). The investigation of the settlement from Thayngen-Weier near Schaffhausen, which belongs to the Michelsberg Culture, brought to light the leafy shoots of elm, birch, oak, lime and maple (GUYAN, 1955, p. 262). Consequently, Troels-Smith ascribes the fall in the *Ulmus* curve, which both in his Danish and Swiss diagrams can be seen at the level where the first indications of a farmer culture appear, to the interference of Neolithic man.

In the Bargeroosterveld I diagram (Fig. 5) *Plantago lanceolata* is very scarce between samples 20 and 35, whereas the pollen of cerealia is present. In sample 19 a pollen grain of *Plantago major* was met with. Simultaneously with the appearance of these indicators of a farmer culture the elm curve shows a recession. The same can be observed in other diagrams from this region (Figs. 6 and 7).

Undoubtedly the agricultural practices of the first farmers in

Drenthe would have shown a great similarity to those in Denmark and Switzerland described by Troels–Smith. In order to obtain arable land people had to make a forest clearing. The size of the fields would have been relatively small. When, after some time, the soil became exhausted, another part of the forest was cleared, whereas on the abandoned field the wood could regenerate. The probably not very numerous livestock would have been allowed to graze on the open places around the settlement—as the abandoned fields—and perhaps also in the forest. An important cattle fodder was constituted by the leafy branches of various deciduous trees.

From the fact that in the Bargeroosterveld I diagram the *Ulmus* percentages again attain their original value between samples 29 and 35, it may perhaps be concluded that at that time these surroundings were unused or at least less intensively utilized.

In the part of the Bargeroosterveld I diagram discussed up to now the course of the curve for *Tilia* shows much resemblance to that for *Ulmus*. For that reason one will ask whether this is to be ascribed to the cutting of the branches of the lime. It has already been noted that in the diagrams Emmen I and V, which provide a general picture of the vegetational history of the whole Emmen district, a marked decrease of *Ulmus* can be seen at the appearance of the first pollen grains of *Plantago lanceolata*. However, in neither of these diagrams is the decline of *Ulmus* attended by a recession of *Tilia*. The fact that generally one observes only a fall of *Ulmus* can perhaps be explained in the following manner. VE (1930) reports that *Fraxinus* flowers again 2 to 3 years after the cutting of the leafy branches, and that after 4 years this tree shows an abundant fruit formation. New shoots of the lime flower after about 4 years. Those of the elm, on the other hand, are unable to produce flower buds in less than 7 or 8 years, and before that time they are mostly cut again. Concerning the other deciduous trees in this respect the present writer has no data at his disposal. If, however, the new shoots of these trees are able to flower after about 4 years, it would be understandable that in consequence of the cutting of leafy branches by prehistoric man the share of *Ulmus* in the pollen rain would decrease considerably more than that of the other trees.

As already mentioned, the Bargeroosterveld I diagram does show a reaction of *Tilia* to the activity of the first farmers. From the fact that in the lower part of this diagram the *Tilia* percentages are about twice as high as those in the corresponding part of the diagrams Emmen I and V it can be concluded that in Atlantic time the forest within a short distance of the Bargeroosterveld profile was particularly rich in lime. It is not impossible that in this forest type lime was the dominant tree.

The course of the curve for *Tilia* could point to a certain predilection of the first farmers for this lime-rich forest, that their settlement was situated within it. The making of clearances in this local forest type can to a certain extent be held responsible for the temporary decrease of *Tilia*. Herewith it has to be considered that the cultivated

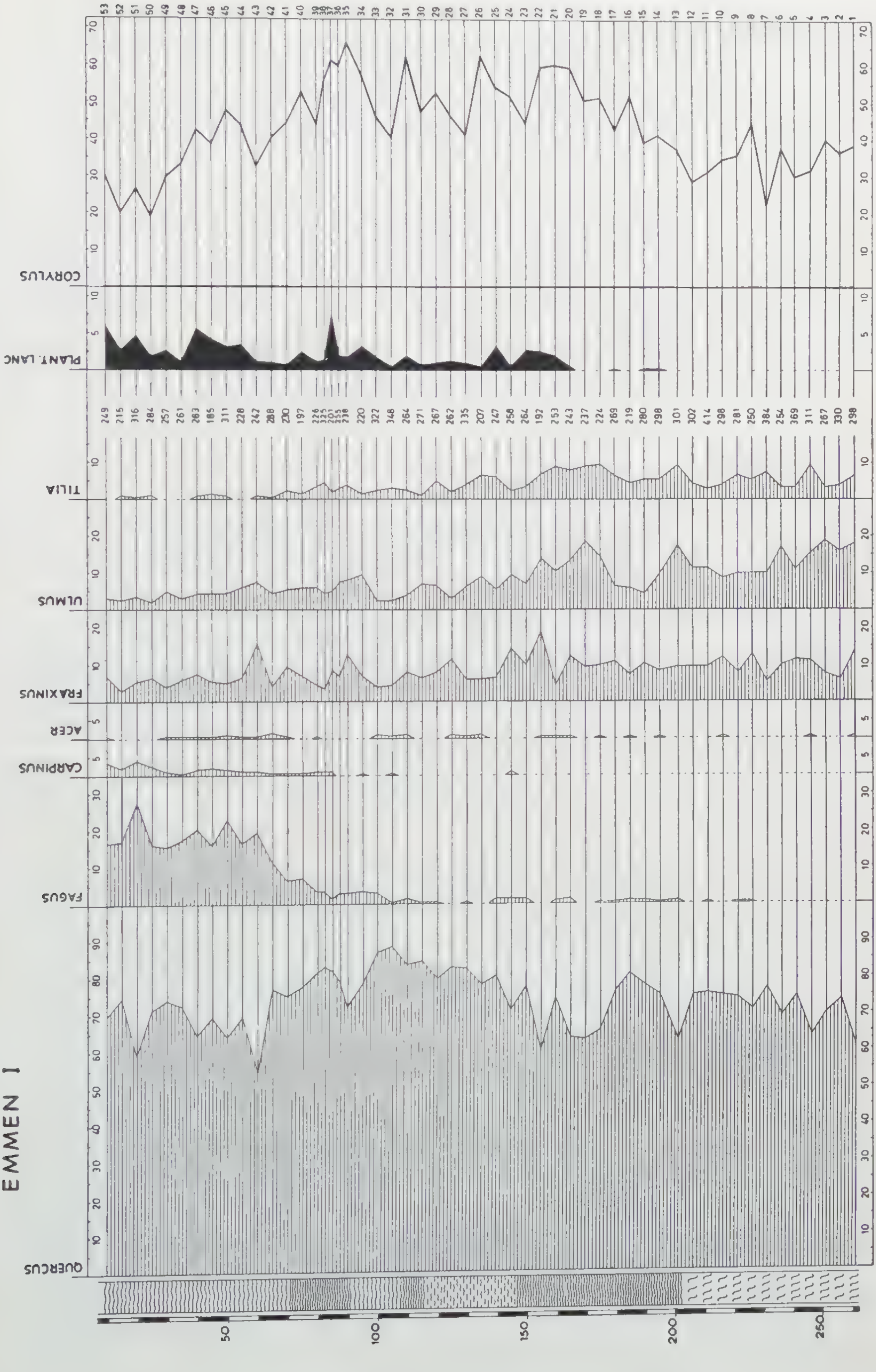
EMMEN I
CORYLUS
PLANT. LANC
TILIA
ULMUS
FRAXINUS
ACER
CARPINUS
FAGUS
QUERCUS
50
100
150
200
250

Fig. 6.

area would not have been great, but that after the exhaustion of each plot of arable land another part of the forest would have been cleared. Moreover, the gathering of cattle fodder would have played a part. Obviously, in the immediate surroundings of the settlement the cutting of branches would have been more intensive than in forests somewhat further away.

One may ask whether the decline of *Ulmus*—if it was the effect of human interference—can be maintained as a criterion for defining the Atlantic/Subboreal border. Although theoretical objections can be raised, it is likely that in practice the recession of *Ulmus* can indeed be so used, at least in western and north-western Europe. The radiocarbon dates published so far suggest that the fall of *Ulmus* was a rather synchronous phenomenon in that area (see Table I).

TABLE I

Radiocarbon dates of the decline of *Ulmus*. The last two dates are of culture layers of the Ertebølle and Early Cortaillod Cultures respectively.

Germany:			
Tannenhausen, Ostfr.	3030 ± 120 B.C.	start of the decline of *Ulmus*	Grohne, 1957*a*
Netherlands:			
Vriezenveen, Overijsel	3030 ± 140 B.C.		Florschütz, 1957
Emmen, Drenthe	3010 ± 135 B.C.		Van Zeist, 1955*b*
England:			
Scaleby Moss, Cumberl.	3015 ± 70 B.C.	end of the decline of *Ulmus*	Godwin, Walker & Willis, 1957
Denmark:			
Aamosen, Zealand	2620 ± 80 B.C.	at some distance above the fall of *Ulmus*	Troels-Smith, 1956
Switzerland:			
Egolzwil, Lucerne	2740 ± 90 B.C.		Troels-Smith, 1956

Although, then, this behaviour of *Ulmus* seemingly cannot be credited to a climatological cause, it still marks a change in climate in western and north-western Europe. For, it will be difficult to explain the decrease of *Hedera*—which in various regions took place simultaneously with the fall of *Ulmus*—otherwise than as the effect of an alteration of climate.

It is not impossible that in the löss area of central Europe the fall of *Ulmus* took place even before 3000 B.C. From about 4000 B.C. this area was occupied by the farmers of the *Bandkeramik* Culture. On the basis of the results of botanical investigations one may assume that agriculture had already reached a high level among these farmers (*cf.* Rothmaler, 1956). Moreover, some cattle was raised, as appears from the rather scarce finds of bones (*cf.* Buttler, 1938, pp. 53–4). The farming practices of this people would not have differed much from those of the first farmers in Switzerland and Denmark. For that reason one has to take into account the possibility that in the löss area of central Europe—which is poor in peat deposits—the decline of *Ulmus* may have taken place before 3000 B.C.

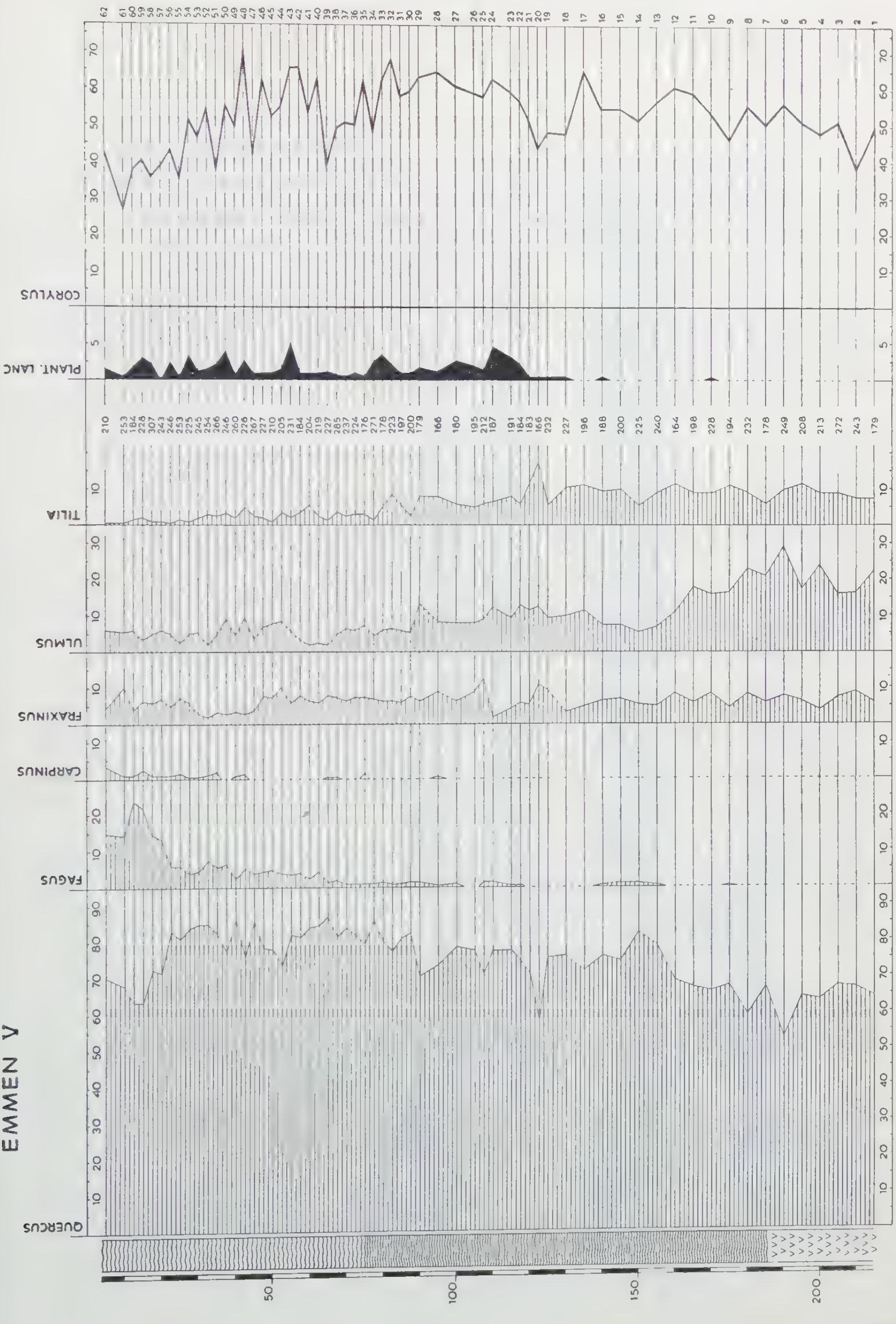
EMMEN V
CORYLUS
PLANT. LANC
TILIA
ULMUS
FRAXINUS
CARPINUS
FAGUS
QUERCUS
10
20
30
40
50
60
70
80
90
50
100
150
200

Fig. 7.

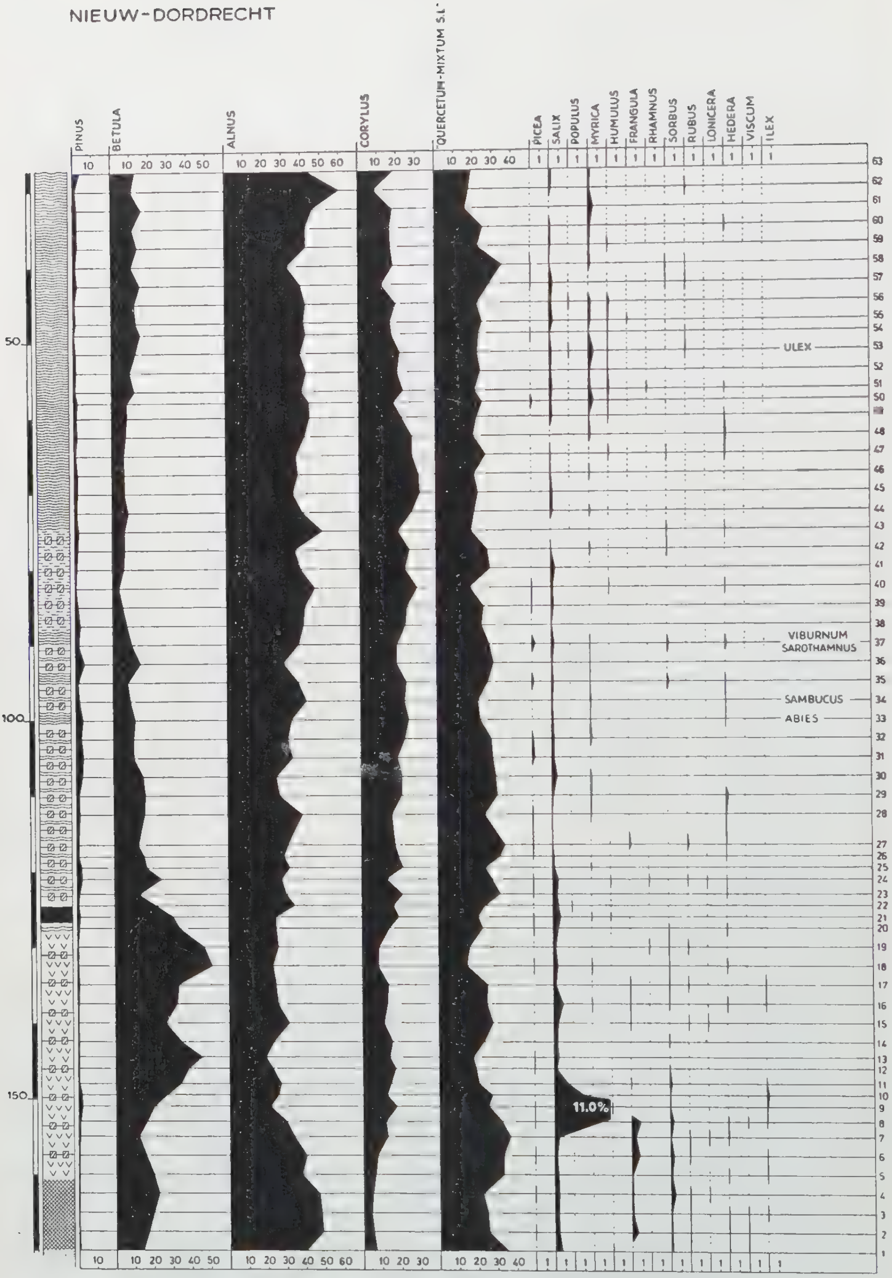

Fig. 8. The stratigraphical position of the Neolithic trackway (*cf.* p. 156) is indicated by a black rectangle on the left side.

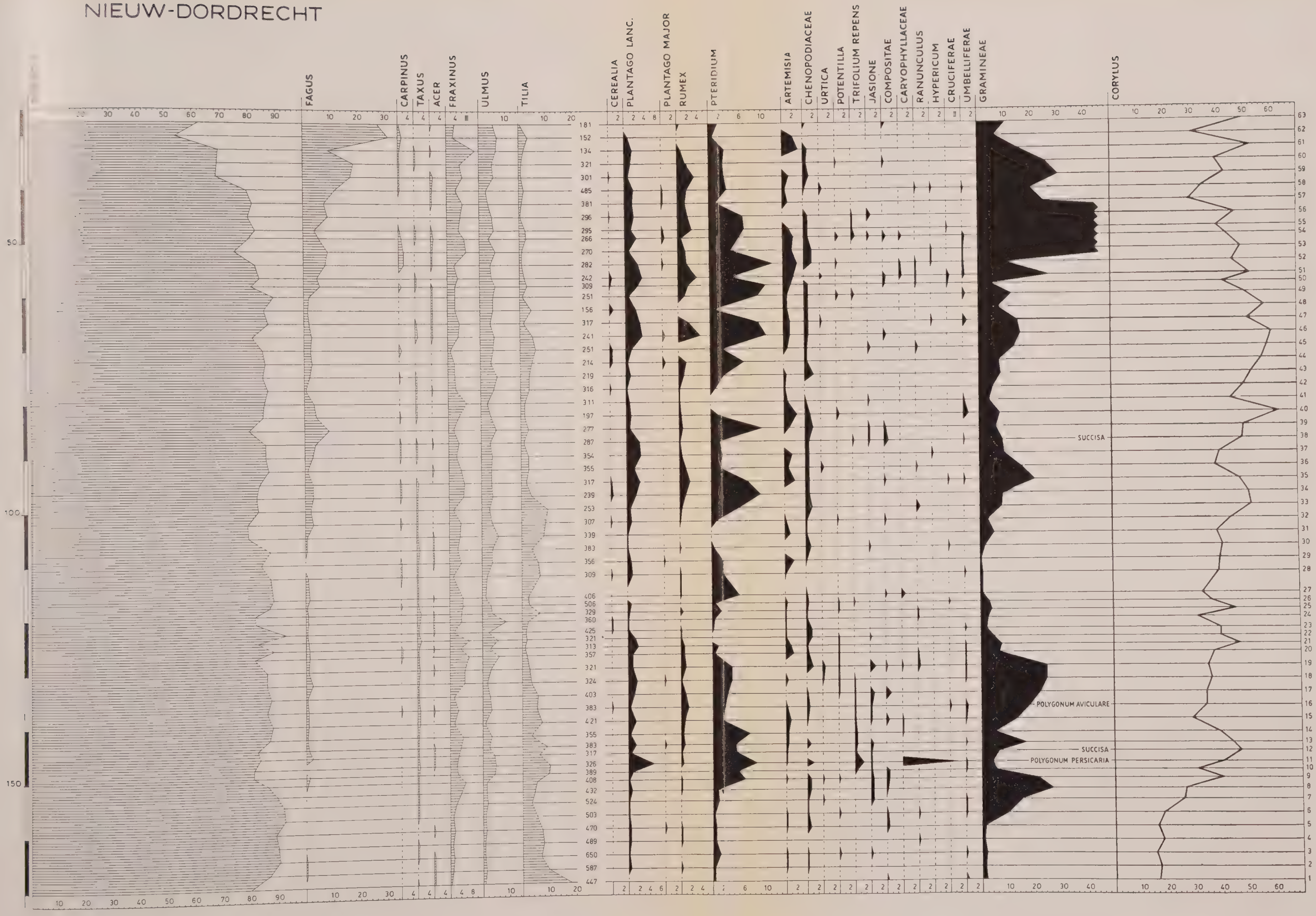
NIEUW-DORDRECHT
FAGUS
CARPINUS
TAXUS
ACER
FRAXINUS
ULMUS
TILIA
CEREALIA
PLANTAGO LANC.
PLANTAGO MAJOR
RUMEX
PTERIDIUM
ARTEMISIA
CHENOPODIACEAE
URTICA
POTENTILLA
TRIFOLIUM REPENS
JASIONE
COMPOSITAE
CARYOPHYLLACEAE
RANUNCULUS
HYPERICUM
CRUCIFERAE
UMBELLIFERAE
GRAMINEAE
CORYLUS
SUCCISA
POLYGONUM AVICULARE
SUCCISA
POLYGONUM PERSICARIA
50
100
150
10 20 30 40 50 60 70 80 90
10 20 30
10 20
2 4 6
2 6 10
10 20 30 40
10 20 30 40 50 60

Fig. 9.

THE INFLUENCE OF NEOLITHIC HERDSMEN ON THE VEGETATION

Sample 36 in the Bargeroosterveld I diagram shows a comparatively high value for *Plantago lanceolata*, which in the next samples decreases again. This is the *landnam* type described by IVERSEN (1941). A rather large area was cleared with the help of axe and fire. On a small part of the clearing cereals would have been cultivated, whereas the rest would have been used as grazing land for the numerous cattle. In contrast to the farmers described on p. 160, these new immigrants were herdsmen. In addition to *Plantago lanceolata*, *Rumex* shows an increase in the Bargeroosterveld I diagram. Reasonably one might expect an increase of Gramineous pollen; in fact, perhaps because it is masked by the pollen of the grasses growing on the peat, no such reaction can be seen at this level. Other plants which can be expected in grassland as *Ranunculus*, *Compositae*, *Succisa* and *Caryophyllaceae*, do not show an increase. On the other hand, from now on the pollen of *Trifolium repens*, *Hypericum cf. perforatum* and *Solanum nigrum* is present. *Trifolium repens* is a typical grassland plant which—if not introduced by these herdsmen—at any rate was able to expand now.

Concerning the regeneration of the forest after the *landnam*, in the Bargeroosterveld I diagram only a rather small increase of *Corylus* can be observed in samples 36 to 40. Nothing can be seen of a probable reaction of *Betula*, certainly on account of the fluctuating local production of the pollen of this tree. Thus, in the tree pollen diagram from this profile (Fig. 4) a *Betula* maximum is present in sample 34. From that level a gradual decline of *Betula* takes place up to sample 38, whereas directly above sample 35 a maximum could be expected.

A clear reaction to this *landnam* is shown by *Tilia*. From sample 37 a steep decline in the *Tilia* curve can be seen. Thereafter, one observes a gradual regeneration of the lime, but from sample 46 onwards the pollen frequencies of *Tilia* again decrease. The increase of *Corylus* in samples 43 to 46 indicates that again forest clearing and subsequent regeneration of the forest took place in the Bargeroosterveld area. The fact that the values for *Plantago lanceolata* remain low—in sample 45 not a single pollen grain of plantain was met with—suggests that the herdsmen did not attack the wood in the immediate surroundings of the Bargeroosterveld profile. When the third wave of large-scale forest clearance blew over this area—this time characterized by a marked increase of *Corylus*, *Plantago lanceolata* and *Gramineae*—lime had not yet recovered, so that there could now be no question of a decline of this tree.

After the period of successive forest clearings, a certain recovery of *Tilia* took place in this area. This appears from a diagram not published here which joins that from Bargeroosterveld I. In that diagram *Tilia* again reaches relatively high values, but with the increase of human activity the percentages for this tree fall to insignificance.

The reaction of *Tilia* to the interference of man is very clearly shown in the diagram from Nieuw-Dordrecht (Fig. 9). In samples 11 to 22 the values for *Plantago lanceolata* are relatively high. This indicates that there was a continuous activity of the herdsmen already mentioned on the boulder clay ridge at the southern point of which the samples for the diagram from Nieuw-Dordrecht were collected. The high value for *Plantago lanceolata* in sample 11, which among other things is accompanied by a relatively high percentage for *Trifolium repens*, suggests that at that time the immediate vicinity of this peat profile was cleared. Just above the level of the trackway (*cf.* p. 156) the values for plantain fall considerably. The share of *Tilia* in the forest vegetation on this boulder clay ridge had diminished regularly from sample 11 onwards. In samples 21 and 22 the percentages for lime show a minimum. After that *Tilia* again increases and relatively high percentages can be observed in samples 31 to 33. From sample 34 *Plantago lanceolata* shows a new rise, and at the same time a marked fall in *Tilia* takes place. Between samples 39 and 45, with comparatively low values for *Plantago lanceolata*, lime is recovering in some degree, only to decline again at the next increase of plantain.

The diagram from Nieuw-Dordrecht once more shows clearly that at least in Subboreal time it was man who first of all must be held responsible for the decline of *Tilia* in this region.

On the basis of his investigations in the raised bog of Gifhorn in central Germany, OVERBECK (1952) arrives at the conclusion that there is a correlation between the humidity and the behaviour of *Tilia*. In the diagrams from Gifhorn, *Tilia* shows a fall during the hygroclinous phase in Overbeck's zone IX. In the xeroclinous first part of zone X this tree again increases, to reach finally low values in the next hygroclinous phase. Concerning the Emmen district the following can be remarked in this connection. In the unpublished diagram from Bargeroosterveld mentioned above, *Tilia* attains relatively high values at the beginning of the last part of the Subboreal. That is the part in which *Fagus* shows somewhat higher values (*cf.* Fig. 6, samples 33 to 41). Just at that time the rainfall must have increased (*cf.* p. 176). But in spite of the increased humidity *Tilia* was able to show a certain recovery, so that, at least in this region, there are no direct indications for a correlation between the degree of humidity and the behaviour of lime. If there was such a relation, it was absolutely overshadowed by the influence of man.

During the Subatlantic the *Tilia* percentages show a further decline. The curve becomes discontinuous even if a comparatively large number of pollen grains is counted in each sample (Fig. 10). It is difficult to decide what was the share of man and of climate in the virtual disappearance of *Tilia* from this region. Although at the moment the temperature conditions are still amply sufficient for *Tilia cordata*, it is possible that the decrease of temperature together with the leaching of the soil has effected a recession of lime.

COMPARISON WITH SPECTRA FROM NEOLITHIC GRAVE MONUMENTS

Thus, in the Bargeroosterveld I diagram two Neolithic *landnam* types can be observed; below, that of a farmer culture; above, that of herdsmen. It is interesting to compare these results with those

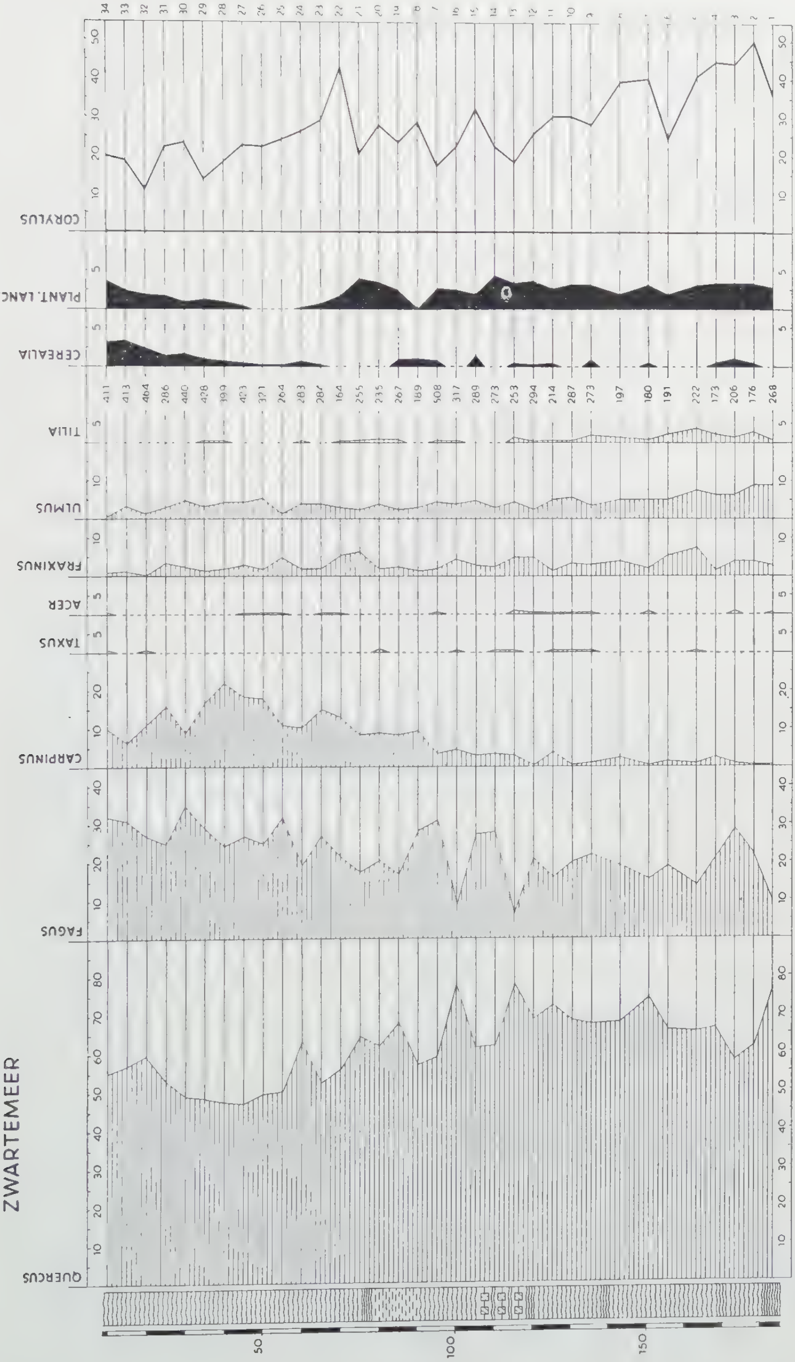
ZWARTEMEER
CORYLUS
PLANT. LANC.
CEREALIA
TILIA
ULMUS
FRAXINUS
ACER
TAXUS
CARPINUS
FAGUS
QUERCUS
411 413 464 286 440 428 399 423 321 264 283 284 164 255 235 267 189 508 317 289 273 253 294 214 287 273 197 180 191 222 173 206 176 268
50
100
150

Fig. 10.

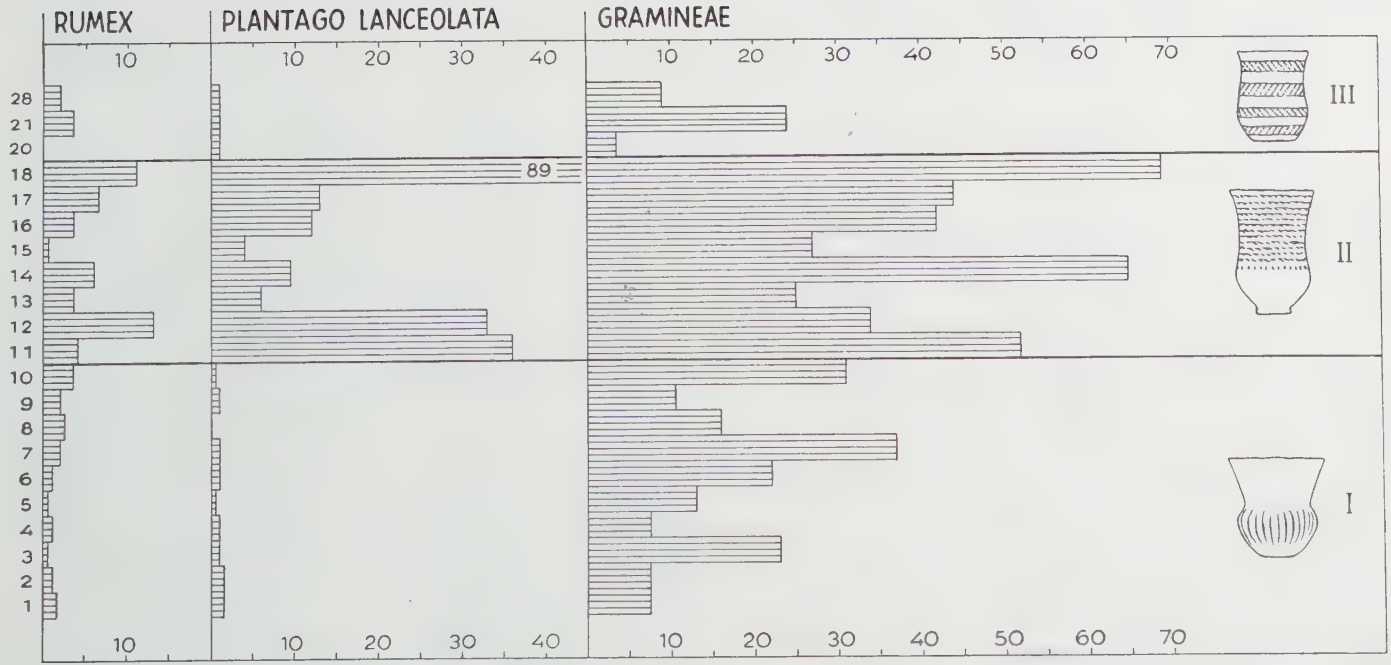

Fig. 11. Some herbaceous pollen percentages in spectra from Neolithic grave monuments in the northern Netherlands. The numbers on the left side refer to those in WATERBOLK's paper (1956). I Funnel Beaker Culture; II Protruding Foot Beaker Culture; III Bell Beaker Culture.

of the palynological investigation of samples from burial monuments of the three Neolithic cultures mentioned on p. 158. As WATERBOLK (1956) has recently published a survey of pollen spectra from Neolithic grave monuments in the northern Netherlands, a few words will suffice here.

As might be expected, the tree pollen frequencies do not show great variations in the samples from the three different groups, in contrast to the percentages for various herbs. In Fig. 11 the frequencies for *Gramineae*, *Plantago lanceolata* and *Rumex* in a number of barrow samples are represented. These are shown as percentages of the total tree pollen sum, *Betula* excluded. From this it appears clearly that the spectra from barrows which belong to the Protruding Foot Beaker Culture are characterized by high values for these herbs. There can be no doubt that the relatively high percentages for *Plantago lanceolata* which in the Bargeroosterveld I diagram occur from sample 36 onwards are to be ascribed to the activity of the people of the Protruding Foot Beaker Culture. The dating of about 2200 B.C. for this level agrees well with the results of some radiocarbon measurements of charcoal from barrows of this culture. It has already been mentioned that in the part of the Bargeroosterveld profile with the relatively high values for plantain some pollen grains of *Solanum nigrum* were met with. It is not impossible that it was the nomadic herdsmen of the Protruding Foot Beaker Culture who brought *Solanum nigrum* with them.

The farmers to whose activity the low values for *Plantago lanceolata* after the decline of *Ulmus* have to be ascribed belong to the Funnel Beaker Culture. The Bell Beaker Culture cannot come into consideration as this people did not arrive here before about 2200 B.C. According to the radiocarbon dating of the decline of *Ulmus* in the Emmen region the first farmers settled at about 3000 B.C. On archaeological grounds, however, this date is considered too early for the beginning of the Funnel Beaker Culture in this area (LÜÜDIK-KAELAS, 1955). For that reason the possibility of a pre-megalithic farmer culture cannot be excluded.

The activity of the farmers of the Bell Beaker Culture does not find expression in the pollen diagram in consequence of the dominating influence of the herdsmen of the Protruding Foot Beaker Culture.

THE BARGEROOSTERVELD II DIAGRAM

Fig. 13 gives an impression of the activity of Bronze Age man in the Bargeroosterveld area. The course of the curve for *Plantago lanceolata* suggests that a *landnam* of the type described by Iversen was not practised. Emphasis would have been on agriculture, whilst cattle would have been allowed to graze on the open places and probably also in the forest. That abandoned fields were used as grazing land appears among other things from the high percentages for *Plantago lanceolata* met with in old surface samples from some Bronze Age barrows in the vicinity of Hijken (VAN ZEIST, 1955a, Table II). The barrows concerned were built on old arable. In view of

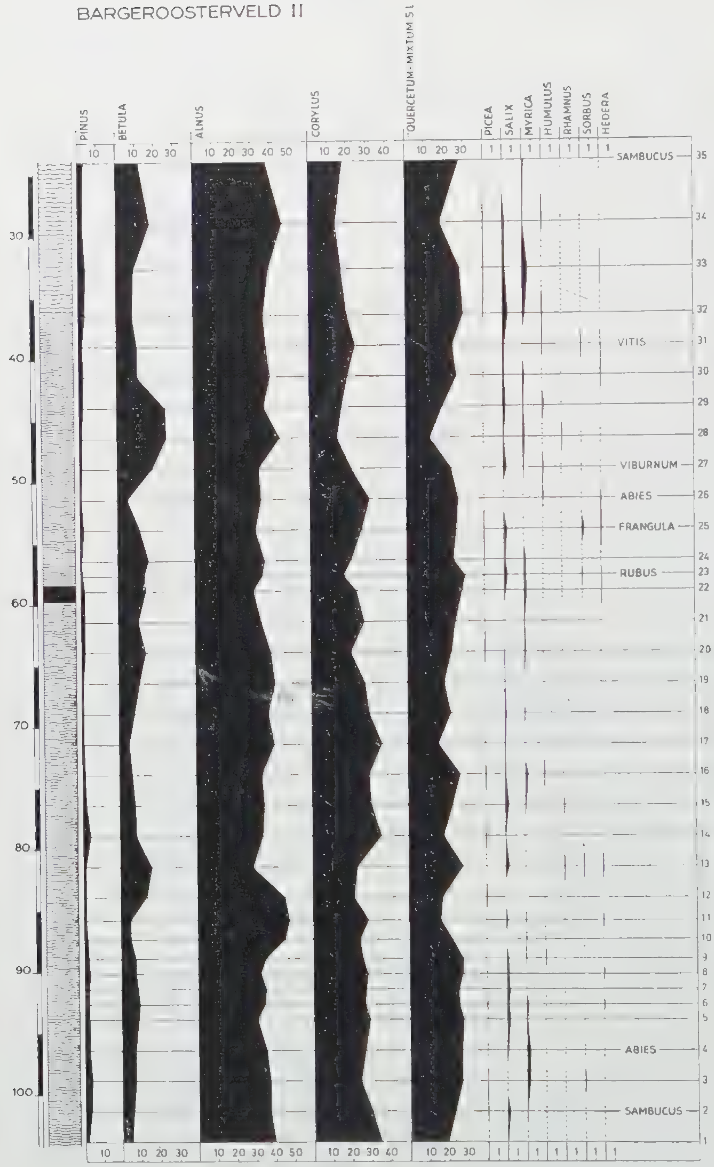

Fig. 12. The stratigraphical position of the wooden structure (*cf.* p. 157) is indicated by a black rectangle on the left side.

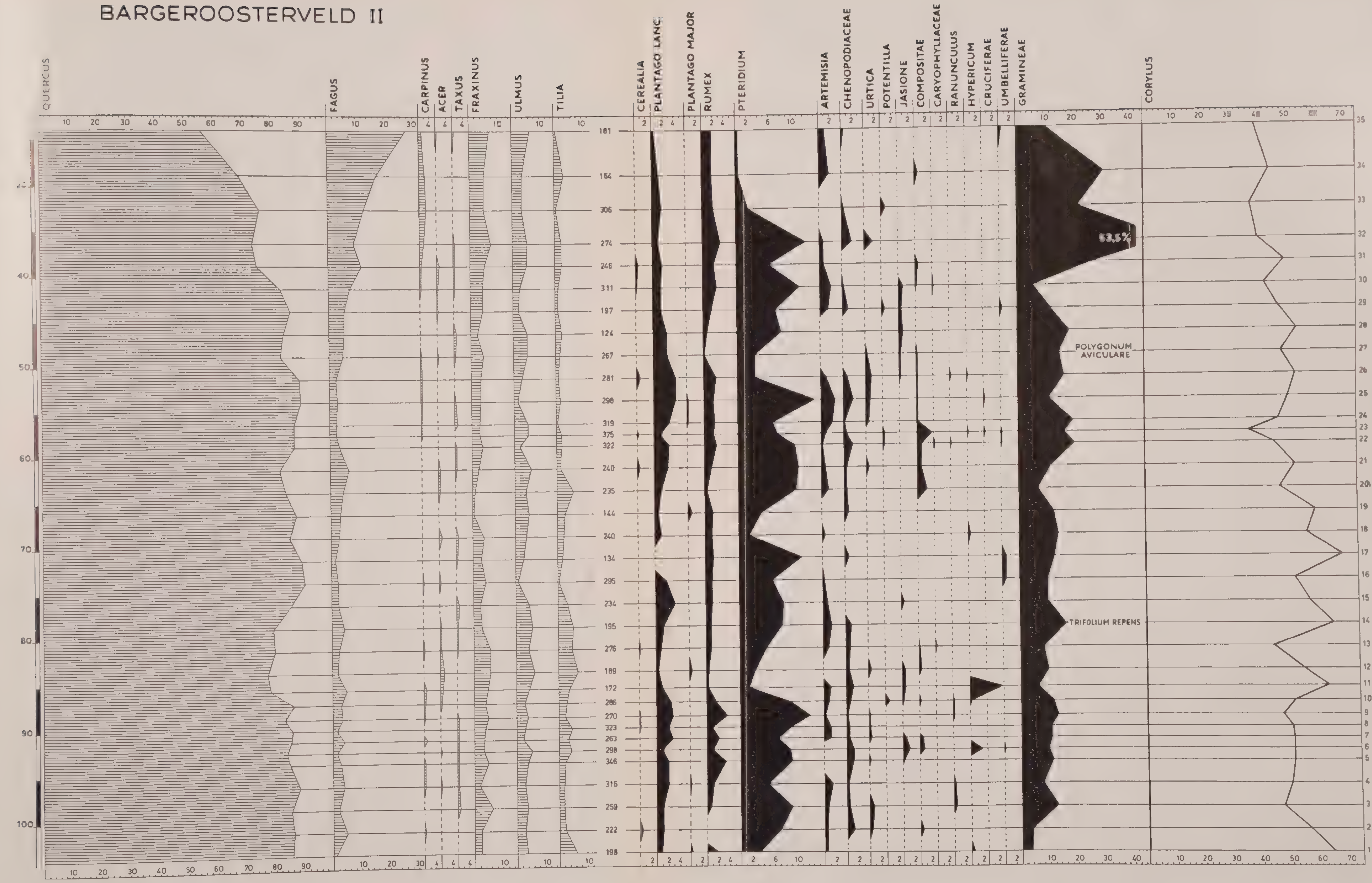
BARGEROOSTERVELD II
QUERCUS
FAGUS
CARPINUS
ACER
TAXUS
FRAXINUS
ULMUS
TILIA
CEREALIA
PLANTAGO LANC.
PLANTAGO MAJOR
RUMEX
PTERIDIUM
ARTEMISIA
CHENOPODIACEAE
URTICA
POTENTILLA
JASIONE
COMPOSITAE
CARYOPHYLLACEAE
RANUNCULUS
HYPERICUM
CRUCIFERAE
UMBELLIFERAE
GRAMINEAE
CORYLUS
53,5%
POLYGONUM AVICULARE
TRIFOLIUM REPENS

Fig. 13.

the dark humous layer which had been formed on top of the arable soil, the fields in question must have been abandoned a fairly long time before the construction of the barrows. Agricultural practice during the Bronze Age would in many respects have resembled that of the Neolithic farmers of the Funnel Beaker Culture. On account of the exhaustive cultivation which was already practised from the beginning of the Neolithic, the conditions for the regeneration of the forest became more unfavourable. In the Bronze Age an expansion of the heather took place. For the present, however, there was no question of large heath lands, which did not originate before mediaeval time.

In the late Subboreal part of the Bargeroosterveld II diagram (Fig. 12, sample 31) a *Vitis* pollen was met with. One pollen grain of *Vitis* could be counted also in the Bronze Age part of the profile from Bargeroosterveld not published here. Moreover, WATERBOLK discovered a pollen grain of *Vitis* in the late-Subboreal part of another profile from the same raised bog (oral communication). These scarce pollen finds of *Vitis* suggest that the grape was cultivated here at least during the Bonze Age.

In the Iron Age and perhaps already in the later part of the Bronze Age more or less permanent arable plots, "Celtic fields", came into use. The increase of the values for *Plantago lanceolata* in the topmost part of the Emmen I diagram (Fig. 6) and the comparatively high percentages for this plant in the lower part of the Zwartemeer diagram (Fig. 10) suggest a more dense population than during the Neolithic and the Bronze Age.

From the investigation of the content of the intestines of some peat burials (HELBAEK, 1950; BRANDT, 1950) it appeared that in addition to cereals, various herbs as *Polygonum aviculare* and *lapathifolium*, *Chenopodium album* and *Spergula arvensis* were eaten by Iron Age man. Besides, during that time the oil-containing seeds of *Linum usitatissimum* and *Camelina sativa* served as food for man.

THE BEHAVIOUR OF FAGUS IN RELATION TO THE HUMIDITY

In the foregoing the behaviour of *Tilia* and *Ulmus* during the second part of the post-glacial in the Emmen area was discussed. We may now consider the other trees of the "*Quercetum-mixtum s.l.*" Concerning the immigration and expansion of *Fagus* in south-eastern Drenthe the following can be remarked. At the end of the Atlantic the first pollen grains of beech appear in peat deposits from this area. During the greater part of the Subboreal, pollen of this tree is regularly met with, provided that a comparatively large number of tree pollen is counted in each sample. As in general the pollen of *Fagus* is not transported over a long distance and, moreover, this tree is underrepresented in the pollen spectrum, it can be assumed that during the first part of the Subboreal the beech was really present in the northern Netherlands, although for a long time it remained rare. Apparently at that time the climate was not very favourable for the beech, so that this tree remained confined to those spots which in edaphic respect were most suited.

A first, but still small expansion of the beech took place in the last part of the Subboreal. In the diagrams in which all trees are included in the tree pollen sum, this increase of *Fagus* is from about 0.3 to 1 %. This level corresponds with the beginning of the continuous *Fagus* curve in most diagrams from north-western Germany. It is notable that this increase of *Fagus* coincided with an increase of precipitation in this area. From the level where *Fagus* shows the increase mentioned above, the formation of slightly humified *Sphagnum cuspidatum* peat (*Vorlaufstorf*) started at various places in the raised bog from south-eastern Drenthe. The *Sphagnum cuspidatum* peat does not form a continuous layer over the whole raised bog, but was deposited in more or less lens-shaped layers. This indicates that the formation of this type of peat took place in pools or at least on very wet spots of various sizes. The only reasonable explanation for this phenomenon is an increase in precipitation, on account of which the conditions for the growth of *Sphagnum cuspidatum* became favourable in the depressions on the surfase of the bog.

A further indication for an increase of precipitation can be seen in the development of a podzol profile under a heather vegetation. In spite of the sometimes fairly high *Calluna* percentages a heather podzol is only exceptionally met with below Neolithic grave monuments. As such exceptions can be mentioned a megalithic tomb near Dötlingen in Oldenburg (Pätzold, 1956) and a Neolithic tumulus (with a Bell Beaker and a *Grand Pressigny* flint dagger) near Witrijt, province of Noord-Brabant (Beex, 1957). On the other hand, below grave monuments from the Bronze and Iron Age a heather podzol is generally present even if the *Calluna* percentages are sometimes rather low. In this connection it has to be remembered that the increase of *Fagus* we are now discussing coincided approximately with the transition from the Neolithic to the Bronze Age.

A further increase of *Fagus* was preceded by another indication of a changing climate. Just before the rise of *Fagus* in the raised bog of south-eastern Drenthe the conditions for the formation of fresh *Sphagnum imbricatum* and *papillosum* peat became favourable. Especially the expansion of *Sphagnum imbricatum* suggests that at that time the moisture of the peat was very high. It is not unlikely that it was not so much a further increase of precipitation as a fall of the temperature which effected an increase of humidity. However that may be, the reaction of *Fagus* to the increased humidity was a considerable expansion. Yet it was not until later that this tree reached its maximal values. This can be seen in the Zwartemeer diagram (Fig. 10), in the upper part of which the percentages for *Fagus* are generally higher than in the lower part. It is probable that it was a further increase of humidity which again effected this last increase of *Fagus*. This may perhaps be concluded from the fact that now the formation of fresh *Sphagnum* peat was in full swing even in the very small raised bogs (*cf.* Waterbolk, 1950). In this respect it must be noted that in consequence of the relatively good drainage the edaphic conditions for the formation of fresh *Sphagnum* peat are not very favourable in these small bogs.

The possibility that beech was also enabled to expand in consequence of the activity of prehistoric man has to be considered here. The beech might have taken advantage of forest regeneration on the abandoned fields. It is clear that in a regenerating vegetation the chances for an expanding species are greater that in a dense forest. If this had been so, a considerable increase of the beech might be expected during the presence of the herdsmen of the Protruding Foot Beaker Culture. For it was these nomads who cleared large parts of the forest, so that during the regeneration of the wood the beech would have been able to expand. This did not, however, happen, or at best very locally. It is true that in the part of the Bargeroosterveld I diagram (Fig. 5) that reflects the activity of the herdsmen of the Protruding Foot Beaker Culture—from sample 36 onwards—the *Fagus* percentages are slightly higher than previously. However, the diagrams Emmen I and V (Figs. 6 and 7) do not show a similar increase of *Fagus* at the corresponding level. Consequently, in the northern Netherlands a general increase of *Fagus* during the period that the people of the Protruding Foot Beaker Culture lived here is out of the question. The rise of *Fagus* took place in the Bronze and Iron Age, and just in these periods much smaller areas were cleared at one time. Besides, in that period a part of the abandoned fields passed into moorland.

In this region the expansion of *Fagus* was therefore certainly not the direct effect of the activity of man. Moreover, if it had been, a more gradual rise of *Fagus* could be expected, whereas the expansion of beech actually took place in a series of jumps.

Concerning the influence of prehistoric man on the living conditions of beech, it may be noted here that a considerable decline of *Fagus* in Switzerland is ascribed to the activity of Neolithic farmers (TROELS-SMITH, 1955).

Summarizing, it can be remarked that in south-eastern Drenthe there must have been a close correlation between the increase of humidity and the expansion of *Fagus*. It appears as if the increasing humidity favoured beech in a direct way. The leaching of the soil, which would have become stronger in consequence of the increase of the humidity, would certainly not have been in favour of the beech. Especially near the border of its areal, this tree makes rather high demands on the soil.

In the Emmen region the expansion of *Fagus* was not directly at the expense of *Tilia* and *Ulmus* (*cf.* FIRBAS, 1949, p. 182). The diagrams from this area show first an important decline of *Ulmus* and *Tilia* in consequence of which the share of the oak in the forest increased. At the level where *Fagus* strongly increases, the *Tilia* values are already very low, whereas during the expansion of *Fagus*, *Ulmus* maintains itself at a certain percentage or at best shows a slight decline. It was the oak at whose expense the beech expanded.

CARPINUS, TAXUS AND ACER IN THE PROFILES EXAMINED

The Zwartemeer diagram (Fig. 10) shows clearly the increase of *Carpinus* in Subatlantic time. During a rather long period, from about 1000 B.C. up to the beginning of the era, this tree was present here in relatively small numbers. After that some expansion took place, although the hornbeam never became as numerous as the beech. It seems that in western Europe the climatological conditions also became more favourable for *Carpinus* in the course of the Subatlantic.

As at first the pollen of *Taxus* was not distinguished, the time of the first appearance of this tree in the northern Netherlands is not yet known with certainty. On the basis of the Bargeroosterveld I diagram (Fig. 5), *Taxus* would have reached this area in the last part of the Atlantic. In contrast to the beech, which arrived here at about the same time, *Taxus* does not show an increase in any period. During the whole Subboreal and Subatlantic the *Taxus* percentages remain very low. However, it is not unlikely that its share in the forest vegetation was more important than the low percentages in the pollen diagram suggest. The sometimes numerous stumps of *Taxus* discovered beneath peat deposits point to this. A survey of these finds is given by FIRBAS (1949, p. 270). This author arrives at the conclusion that in north-western Germany *Taxus* was present at least at the transition from the Atlantic to the Subboreal. This is not in contradiction with the Bargeroosterveld I diagram, which shows the first pollen grains of *Taxus* in the upper part of the Atlantic.

Prehistoric man knew the excellent qualities of *Taxus* wood, as is shown by the shaft for an adze discovered at the excavation of the trackway of Nieuw-Dordrecht (*cf.* p. 156). Radiocarbon measurement of a sample of wood from this trackway dates this object to about 1885 B.C.

Pollen of *Acer* appears in the first part of the Atlantic. Of the three *Acer* species now found in western and north-western Europe, *Acer campestre* is indigenous in the Netherlands, whereas *Acer pseudo-platanus* seems to be native at least in a part of the country. The western limit of *Acer platanoides* lies to the east of the eastern border of the Netherlands (*cf.* GAMS, 1924). As it has thus far appeared impossible to separate the pollen of the various *Acer* species, palynological investigation cannot show which species of this genus grew here in earlier times. It must, however, be noted that under the remains of a house of the 6th to 7th century B.C. near Jemgum, 5 km to the north-west of Leer, a piece of wood of *Acer pseudo-platanus* was found by GROHNE (1957b). From this it may be concluded that at that time *Acer pseudo-platanus* would have occurred likewise in the northern Netherlands. As with *Taxus* the *Acer* percentages remain very low.

Acer platanoides is a subcontinental species (FIRBAS, 1949, p. 185), so that it is likely that at least during the post-glacial this tree did not occur in the Netherlands, assuming that the Subboreal did not have a comparatively continental character (see below).

HEDERA, VISCUM AND ILEX IN THE EMMEN DISTRICT

Finally, the occurrence of *Hedera*, *Viscum* and *Ilex* in the pollen diagrams presented in this paper will be discussed. On the basis of the present distribution of *Hedera*, *Viscum* and *Ilex* and the temperature data of a number of meteorological stations relevant to this purpose, IVERSEN (1944) was able to construct thermal correlation diagrams for each of these plants. Therewith it was assumed that the mean temperature for the warmest and coldest months provides a good idea of the course of the temperature during the whole year. Iversen could demonstrate that the northern and eastern limit of these plants is determined by the temperature. The occurrence of *Viscum* appears especially to be dependent on the mean temperature during the warmest month. This plant can endure fairly much cold during the winter. This in contrast to *Ilex* and *Hedera*, for which the mean temperature of the coldest month rather quickly becomes a limiting factor. On the other hand, these plants are able to thrive at lower summer temperatures than *Viscum*.

From the frequencies of *Hedera*, *Viscum* and *Ilex* in the material studied by him, Iversen concluded that during the Atlantic the mean January and July temperatures were 0.5° and 2° C higher than nowadays. During the Subboreal the mean January temperature would have been 1° C lower and the mean July temperature 2° C higher than at present. Consequently, the Subboreal climate would have had a more continental character than that of the Atlantic and Subatlantic. The greater part of the material studied by Iversen was collected in Djursland, in eastern Jutland, with mean January and July temperatures of 0° and 16° C respectively.

However, the results of HAFSTEN (1956, 1957) in the rather continental Oslo Fjord area could point to a somewhat different course of the temperature. In that area the temperature conditions are such that at present *Hedera* and *Viscum* cannot grow there. In the Atlantic and also in the Subboreal, *Hedera* and *Viscum* were present in the Oslo Fjord area, although for the latter period the percentages are considerably lower. Hafsten arrives at the conclusion that at present the mean January temperature must be at least 2° C lower than during the Atlantic and the Subboreal. A more continental Subboreal, compared with the present climate, can hardly have been the case in the Oslo Fjord area. The behaviour of *Hedera* and *Viscum* in that area can only be explained by assuming a more or less gradual decrease both in the summer and the winter temperature.

Now, Iversen's "continental" Subboreal is mainly based on the fact that in his material *Ilex* is totally lacking. He assumes that in the Atlantic this plant did not yet reach Djursland, whereas during the Subboreal the climate, that is to say the winter temperature, would have been too unfavourable for *Ilex*. The fact that *Ilex* pollen was not found in the Subatlantic material is ascribed by Iversen to the relatively small number of pollen grains counted from this period. In this connection it has to be remembered that nowadays *Ilex* is present in Denmark.

On the other hand, one has to take into account the possibility that the absence of *Ilex* was not so much due to climatological as to ecological factors; that this tree did not get the chance to establish itself in the dense forests on the fertile moraine soils of Djursland. If a gradual fall in both the summer and the winter temperature is also assumed for Denmark, the considerable decline of *Viscum* in the course of the Subboreal can better be understood. On the ground of Iversen's hypothesis practically no decline of *Viscum* might have been expected during the Subboreal.

TABLE II

Occurrence of *Hedera*, *Viscum* and *Ilex* in the profiles discussed in this paper.

	samples	$\sum$ *Quercus Ulmus Fraxinus Tilia Fagus Carpinus*	*Hedera*			*Viscum*			*Ilex*		
			no. of pollen of	no. of samples with	percentage	no. of pollen of	no. of samples with	percentage	no. of pollen of	no. of samples with	percentage
Emmen I											
Subatlantic	42–53	3085	3	3	0.10	—	—	—	—	–	—
Subboreal 2	33–41	2209	3	3	0.14	—		—	–	–	—
Subboreal 1	14–32	4924	20	14	0.41	2	2	0.04	3	3	0.06
Atlantic	1–13	4055	13	9	0.32	1	1	0.02	—	—	—
Emmen V											
Subboreal 2	40–56	3968	7	5	0.18	—	—	—	1	1	0.03
Subboreal 1	12–39	5733	18	13	0.31	—	—	—	—	—	–
Atlantic	1–11	2394	6	6	0.25	1	1	0.04	—	—	—
Zwartemeer											
Subatlantic	2–34	9549	5	5	0.05	1	1	0.01	2	2	0.02
Nieuw-Dordrecht											
Subboreal 2	32–57	7163	12	10	0.17	—	—	—	—	–	—
Subboreal 1	1–31	12448	19	15	0.15	4	4	0.03	16	9	0.13
Bargeroosterveld I											
Subboreal 2	61–82*	5584	7	7	0.13	—	—	—	1	1	0.02
Subboreal 1	19–60	11326	21	16	0.19	8	8	0.07	11	3	0.10
Atlantic	1–18	4494	21	9	0.47	11	5	0.24	—	—	—
	[6–18	3372	8	4	0.24]						
Bargeroosterveld II											
Subboreal 2	1–30	7581	9	9	0.12	—	—	—	—	—	–

* The upper part of the Bargeroosterveld I diagram is not published in this paper.

From the occurrence of *Emys orbicularis* (Degerbøl and Krog, 1951) and some insects as *Potosia speciosissima* (Johnsen and Krog, 1948) and *Cerambyx cerdox* (Thomsen and Krog, 1949) in Subboreal deposits from Denmark, it may be concluded that during that period the mean July temperature must have been at least 18° C there. If the hypothesis put forward above is correct, during the Atlantic the mean temperature for the warmest month in most parts of Denmark must have been still higher (*cf.* IVERSEN, 1944, Fig. 9).

Concerning the gradual fall of the temperature after the climatic optimum in the Atlantic, this "gradual" is not to be understood too literally. Undoubtedly there would have been minor oscillations, in consequence of which the general decline of the temperature might have been intensified, weakened or even totally reversed. On account of the influence of the sea, the fall of the temperature would have been of less importance in oceanic regions than in more continental areas.

The data concerning *Hedera*, *Viscum* and *Ilex* from the profiles discussed in this paper are represented in Table II. The average pollen frequencies for these plants are shown as percentages of the sum of *Quercus*, *Tilia*, *Ulmus*, *Fraxinus*, *Fagus* and *Carpinus*. The total number of tree pollen counted in this material is about 380 000. It appeared useful to divide the Subboreal into two parts. In the lower part (Subboreal 1) the *Fagus* percentages are very low, in the upper one (Subboreal 2) *Fagus* shows somewhat higher values (about 1 % in the diagrams in which all trees are included in the tree pollen sum). At present the Emmen district has mean January and July temperatures of about 1° and 16° C respectively (BRAAK, 1950).

The *Hedera* percentages in the diagrams Emmen I and V do not show great mutual differences. The graph of Fig. 14 is drawn from the data of both these diagrams, and completed with the results of the Zwartemeer profile for the Subatlantic. As in the first part of the Subatlantic the percentages for *Hedera* are somewhat higher than in the later phases of this period the Subatlantic part of the Emmen I diagram is not included in this graph.

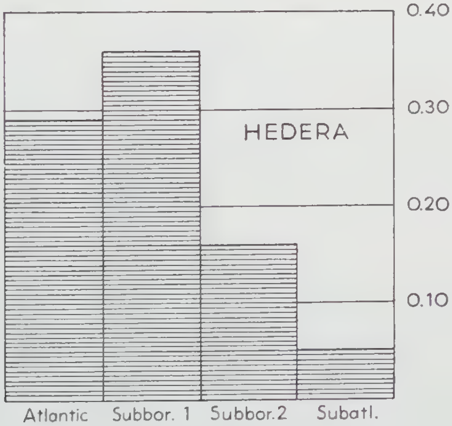

Fig. 14. Graph of the *Hedera* values in the diagrams Zwartemeer, Emmen I and V.

In the diagrams Emmen I and V there is no question of a fall of *Hedera* at the transition from the Atlantic to the Subboreal. This is clearly shown in the graph. On the other hand, the Atlantic part of the Bargeroosterveld I diagram does show a considerably higher *Hedera* value than the next periods. However, this relatively high *Hedera* percentage is to a large extent effected by 13 pollen grains of this plant counted in the lowermost 5 samples. If these samples are left out of consideration (the values in brackets) the *Hedera* percentage in the last part of the Atlantic does not longer show a significant difference with that in the next period. Very probably the relatively high *Hedera* value in the lower samples from this profile reflects a very local occurrence of this liane. That in general the *Hedera* values in the diagrams from Bargeroosterveld and Nieuw-Dordrecht have a more local character appears also from the circumstance that in these diagrams the *Hedera* percentages in the first part of the Subboreal are considerably lower than in the diagrams Emmen I and V. Undoubtedly the Emmen diagrams give a better reflection of the behaviour of *Hedera* in the Emmen district than those of Bargeroosterveld and Nieuw-Dordrecht. In these latter diagrams little or nothing can be seen of the fall of *Hedera* which is very pronounced in the graph of Fig. 14.

That *Hedera* does not show a decline at the transition from the Atlantic to the Subboreal need not mean that here no change of climate had set in at that time. A plant will not react to a change in its environment before a critical point has been reached. Thus it is possible that at first the fall in temperature had no influence on the frequency of ivy in the northern Netherlands.

Concerning the marked decline of *Hedera* in the last part of the Subboreal, this could indicate that the fall in temperature had now proceeded so far that *Hedera* decreased. On the other hand, it is perhaps possible that the increased precipitation in the last part of the Subboreal (*cf.* p. 176) affected unfavourably the dispersal of the pollen of *Hedera*. For this plant flowers in the Autumn, during which season there would undoubtedly have been much rain.

The further decline of *Hedera* in the Subatlantic agrees with the behaviour of this plant in the other parts of western and north-western Europe.

The *Viscum* values in the diagrams from the more central part of the raised bog are so low that on the ground of the available material it is not possible to draw conclusions concerning a possible decline of this semi-parasite. There is reason to suppose that it is not wise to conclude from these very low values that in this region *Viscum* was always an extremely rare plant. In the lower part of the Bargeroosterveld I profile *Viscum* occurs fairly regularly. In sample 13 5 pollen grains of this plant were counted. *Viscum* likewise occurs regularly in the lower part of the Buinerbrug diagram (WATERBOLK, 1954, Fig. 16). Peat deposits which were formed at a short distance from the higher soils can contain a relatively large number of *Viscum* pollen. This points to a very poor dispersal of *Viscum* pollen over distances.

As with *Viscum*, pollen of *Ilex* was in general rarely met with. Consequently, the few counted pollen grains do not allow conclusions. However, in certain forest types *Ilex* would have been fairly common. Thus in the lower part of the Nieuw-Dordrecht diagram *Ilex* pollen occurs regularly, indicating that this tree was not uncommon in the forest on the most south-eastern offshoot of the Hondsrug. That *Ilex* pollen is lacking in the upper part of this profile is probably due to the expansion of the peat, thus increasing the distance between the spot where the profile was sampled and the forest in which holly grew.

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The author wishes to thank Professor Dr. H. T. Waterbolk for critical reading the manuscript. He is also indebted to Miss L. van Duinen for technical assistance and to Mr. B. Kuitert and Mr. H. Roelink for drawing the diagrams. Finally his thanks are due to Dr. J. J. Butler for the correction of the English text.

REFERENCES

BEEX, G. 1957. Een neolithische grafheuvel met beker en vuursteendolk bij de Witrijt (gem. Bergeijk). Bijdragen tot de studie van het Brabantse Heem. Deel IX: 7–23.

BRAAK, C. 1950. Het klimaat van Nederland. Den Haag.

BRANDT, I. 1950. Planterester i et Moselig fra Borremose. Aarbøger for nordisk Oldkyndighed og Historie 1950: 342–51.

BROCKMANN-JEROSCH, H. 1918. Das Lauben und sein Einfluss auf die Vegetation der Schweiz. Mitteilungen der Geographisch-Ethnographischen Gesellschaft Zürich **18**: 131–50.

BUTTLER, W. 1938. Der donauländische und der westische Kulturkreis der Jüngeren Steinzeit. Handbuch der Urgeschichte Deutschlands. Band **2**.

DEGERBØL, M. og H. KROG. 1951. Den europaeiske Sumpskildpadde (*Emys orbicularis* L.) i Danmark. Danmarks Geologiske Undersøgelse. II. Raekke. Nr. 78.

FAEGRI, K. 1940. Quartärgeologische Untersuchungen im westlichen Norwegen. II Zur spätquartären Geschichte Jaerens. Bergens Museums Aarbok 1939–40. Naturvit. rekke Nr. 7.

———. 1944*a*. Studies on the Pleistocene of Western Norway. III Bømlo. Bergens Museums Aarbok 1943. Naturvit. rekke Nr. 8.

———. 1944*b*. On the Introduction of Agriculture in Western Norway. Geol. Fören. Förhandl. **66**: 449–62.

FIRBAS, F. 1949. Spät- und nacheiszeitliche Waldgeschichte Mitteleuropas nördlich der Alpen. Band I: Allgemeine Waldgeschichte. Jena.

FLORSCHÜTZ, F. 1957. Over twee "geijkte" pollen- en sporendiagrammen uit de omgeving van Vriezenveen. Boor en Spade **8**: 174–8.

GAMS, H. 1924. *Aceraceae*. In: G. HEGI. Illustrierte Flora von Mittel-Europa. Band V, 1. München.

GODWIN, H. 1956. The History of the British Flora. A Factual Basis for Phytogeography. Cambridge.

———, D. WALKER and E. H. WILLIS. 1957. Radiocarbon dating and postglacial vegetational history: Scaleby Moss. Proc. Roy. Soc. B **147**: 352–66.

GROHNE, U. 1957*a*. Zur Entwicklungsgeschichte des ostfriesischen Küstengebietes auf Grund botanischer Untersuchungen. Probleme der Küstenforschung im südlichen Nordseegebiet **6**: 1–48.

———. 1957*b*. Botanische Untersuchung der vorgeschichtlichen Siedlung Jemgum a. d. Ems. Die Kunde N. F. **8**: 44–52.

GUYAN, W. U. 1955. Das jungsteinzeitliche Moordorf von Thayngen-Weier. In: Das Pfahlbauproblem. Basel. 223–72.

HAFSTEN, U. 1956. Pollen-Analytic Investigations on the Late Quaternary Development in the Inner Oslofjord Area. Universitet i Bergen. Aarbok 1956. Naturvit. rekke Nr. 8.

————. 1957. Om mistelteinens og bergflettens historie i Norge. Blyttia **15**: 43–60.

HEER, O. 1865. Die Pflanzen der Pfahlbauten. Neujahrsblatt der Naturforschenden Gesellschaft auf das Jahr 1866: 1–54.

HELBAEK, H. 1950. Tollund Mandens sidste Maaltid. Aarbøger for nordisk Oldkyndighed og Historie 1950: 311–41.

IVERSEN, J. 1941. Landnam i Danmarks Stenalder. Danmarks Geologiske Undersøgelse. II. Raekke. Nr. 66.

————. 1944. *Viscum*, *Hedera* and *Ilex* as Climate Indicators. Geol. Fören. Förhandl. **66**: 463–83.

JOHNSEN, P. and H. KROG. 1948. *Potosia speciosissima* Scop. subfossil in Denmark (*Coleoptera Lamellicornia*). Ent. Medd. **25**: 252–62.

LÜÜDIK-KAELAS, L. 1955. Wann sind die ersten Megalithgräber in Holland entstanden? Palaeohistoria **4**: 47–79.

MITCHELL, G. F. 1951. Studies in Irish Quaternary Deposits: No. 7. Proc. Roy. Irish Acad. **53**B: 111–206.

————. 1956. Post-Boreal Pollen-Diagrams from Irish Raised-Bogs. Proc. Roy. Irish Acad. **57**B: 185–251.

OVERBECK, F. 1952. Das grosse Moor bei Gifhorn im Wechsel hygrokliner und xerokliner Phasen der nordwestdeutschen Hochmoorentwicklung. Bremen-Horn.

PÄTZOLD, J. 1956. Das 4000 jährige Steingrab von Dötlingen. Nordwest Heimat. Beilage zu Nr. 193 der "Nordwest-Zeitung", Nr. 15/56.

ROTHMALER, W. 1956. Der Ackerbau im Neolithikum Mitteleuropas. Ausgrabungen und Funde **1**: 51–3.

THOMSEN, M. og H. KROG. 1949. *Cerambyx cerdo* L. (= *heros* Scop.) fra subboreal Tid i Danmark. Vidensk. Medd. fra Dansk naturh. Foren. **111**: 131–48.

TROELS-SMITH, J. 1953. Ertebøllekultur—Bondekultur. Aarbøger for Nordisk Oldkyndighed og Historie 1953: 5–62.

————. 1955. Pollenanalytische Untersuchungen zu einigen schweizerischen Pfahlbauproblemen. In: Das Pfahlbauproblem. Basel. 11–58.

————. 1956. Neolithic Period in Switzerland and Denmark. Science **124**: 876–81.

TÜXEN, R. 1955. Das System der nordwestdeutschen Pflanzengesellschaften. Mitteilungen der Floristisch-soziologischen Arbeitsgemeinschaft N.F. **5**: 155–76.

VE, S. 1930. Skogtraernes forekomst og høidegrenser i Aardal. Meddelelser fra Vestlandest Forstlige Forsøksstation. Bd. **4**, H. 3. Medd. Nr. 13.

WAALS, J. D. VAN DER and W. GLASBERGEN. 1955. Beaker Types and their Distribution in the Netherlands. Palaeohistoria **4**: 5–46.

WATERBOLK, H. T. 1950. Palynologisch onderzoek van de versterking bij het Witteveen en de cultuursporen in het Bolleveen, beide bij Zeijen, gem. Vries. Nieuwe Drentse Volksalmanak **68**: 100–21.

————. 1954. De praehistorische mens en zijn milieu. Thesis Groningen.

————. 1956. Pollen Spectra from Neolithic Grave Monuments in the Northern Netherlands. Palaeohistoria **5**: 39–51.

WIERINGA, J. 1958. Opmerkingen over het verband tussen de bodemgesteldheid en oudheidkundige verschijnselen naar aanleiding van de Nebokartering in Drente. Boor en Spade **9**: 97–114.

ZEIST, W. VAN. 1955*a*. Pollen Analytical Investigations in the Northern Netherlands. Acta Bot. Neerl. **4**: 1–81.

————. 1955*b*. Some Radio-Carbon Dates from the Raised Bog near Emmen (Netherlands). Palaeohistoria **4**: 113–8.

————. 1956*a*. De veenbrug van Nieuw-Dordrecht. Nieuwe Drentse Volksalmanak **74**: 314–8.

————. 1956*b*. Die palynologische Bearbeitung des Münzfundes von Barger-compascuum. Palaeohistoria **5**: 93–9.

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BRIEF REPORTS

JONKER, F. P.: Hypericum canadense in Europe

In 1935 the present author reported the occurrence of this N. American species in the eastern part of Holland, province of Overijssel, in the vicinity of Almelo (Jonker, 1935). He found the species near the hamlet of Harbrinkhoek on a wet heath. The locality was also the only station of *Wahlenbergia hederacea* in the Netherlands, discovered a year before. Notwithstanding the extensive reclamations in that part of the country the species now still occurs in a number of localities around Almelo. The plants cannot be considered adventitious as they were found in places that are comparatively little influenced by human culture, judging from the occurrence, on the first-discovered locality, of e.g. *Wahlenbergia hederacea, Gentiana pneumonanthe, Viola palustris, Radiola linoides, Linum catharticum, Scutellaria minor*. The late Dr. Wachter discovered, in the herbarium of the Royal Botanical Society of the Netherlands, unidentified specimens of *Hypericum canadense* collected by Lako as early as 1909 in the same environment, perhaps even in the same station; and Dr. van Soest identified two specimens collected in 1918 by the late naturalist Bernink near Denekamp, about 20 km E of the above mentioned localities.

Bouchard (1953, 1954, 1955) reported the discovery of the species in France, dept. Haute-Saône. The plants were found in large quantities, at the stony beach of oligotrophous lakes, together with *Littorella uniflora*. In his detailed publication of 1954 he discussed the possibilities of introduction. He concluded that the plants are not adventitious. They may be autochthonous or naturalized and then, when the latter is the fact, probably by U.S. army units that stayed in that area during world war I. He did not preclude, however, the possibility of a glacial relic. Bouchard overlooked the previous publication reporting the occurrence in Holland.

Webb (1957), who reported the finding of the species in Ireland overlooked both Bouchard's and Jonker's publication, mentioning only the former in a note added during the printing. He discovered a single, poorly developed specimen in 1954 and tried to grow it in his garden. When visiting the locality again, in 1956, he discovered large quantities and consequently was in a position to identify the species. The locality had been visited in 1932 without the species being discovered. Webb is inclined to consider the species a new representative of the American element in the Irish flora. In a later publication he also considered the occurrence in Holland and France (Webb, 1958). In that paper he discussed three possibilities: 1. recent introduction by human agency; 2. a recent arrival by natural means, 3. it is an old-established native. In his opinion the balance of evidence is in favour of supposing that the species is relic in Ireland and on the European continent. McClintock (1958), in the same periodical, added a report of his visit to the locality in August, 1956, and stated that he found the plant in abundance.

Merxmüller and Vollrath (1956) reported the finding, in 1949, of the related N. American *Hypericum majus* (Gray) Britt., formerly considered a variety of *H. canadense*, near Weiden in Germany, in a sand pit where it had been introduced, in all likelihood, by U.S. military units during world war II. They wondered whether Bouchard's plants also belong to that species. But as Bouchard compared his material with specimens from Canada, we should perhaps leave the finding of this related species in Germany out of consideration.

The first-known occurrence in Europe is consequently Holland, 1909, followed by the rediscovery in that country and by discoveries in France and Ireland. The three localities are remote and little influenced by human activities. Moreover, they had not been investigated very thoroughly before.

The present author has discovered the species from 1935 onwards in several localities around Almelo, and thinks it very peculiar that it had been overlooked before, both by him and by other botanists and amateurs. The French locality is not well known. But also in Ireland the species was discovered in a locality in which it was not found in 1932. In 1954, a single specimen was found and in 1956 it occurred in plenty. These facts do not give the impression that the species has recently been introduced into Europe. Possibly it is a relic that had been able to maintain itself in only a few localities in Europe, in contrast to North America where it is rather common. But there are indications that the species has spread intensively around the few European stations during the last 20 years. Reclamations, however, limited this almost explosive expansion, at least in the Netherlands.

REFERENCES

BOUCHARD, J. 1953. Bull. Soc. Hist. Nat. Doubs **57**: 95.
————. 1954. Bull. Soc. Bot. France **101**: 351.
————. 1955. Ann. Sc. Univ. Besançon, 2e Sér. Bot. fasc. 4 et 5: 95.
JONKER, F. P. 1935. Ned. Kruidk. Arch. **45**: 138.
MCCLINTOCK, D. 1958. Watsonia **4**: 145.
MERXMÜLLER, H. und H. VOLLRATH. 1956. Ber. Bay. Bot. Ges. **31**: 130.
WEBB, D. A. 1957. The Ir. Nat. Journ. **12**.5: 113.
————. 1958. Watsonia **4**: 140.

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BOOK REVIEWS

OF PUBLICATIONS RELATED TO BOTANICAL WORK IN THE NETHERLANDS

Lindeboom, G. A.: Haller in Holland. Het dagboek van Albrecht von Haller van zijn verblijf in Holland (1725–1727), pp.106, 1958. Published by the Koninklijke Nederlandsche Gist- en Spiritusfabriek N.V., Delft. A limited number of free copies obtainable on request.

The book starts with a biography of von Haller in Dutch (p. 1–18). Professor Lindeboom here devotes special attention to the relations between Haller and Boerhaave, as the former came to Holland to continue his studies with the Leyden coryphaeus.

The second part (p. 19–106) is the diary which Haller kept during his stay in Holland. This is written in German, and mainly based on the publications of the complete diary, edited by Hirzel (1883) and Hintzsche (1948). It gives numerous remarkable and interesting observations with regard to the life at the famous university and in the town, and of his contact with the professors, especially with Albinus and Boerhaave. He also visited Amsterdam, Utrecht, Groningen, Haarlem and other places. During his stay in Holland he visited a number of gardens of which the garden "Tulpenburg" at Ouderkerk a.d. Amstel especially impressed him. The botanical garden at Leyden was in his opinion the richest in the world, containing ca. 6000 species. His studies in this "Hortus Medicus" and the lectures by Boerhaave in that garden laid the foundations of his later botanical work in Göttingen and in Switzerland.

The get-up of the book is excellent. It contains a number of reproductions of engravings and a portrait as frontispiece. F. P. J.

Frey–Wyssling, A.: Die pflanzliche Zellwand, 1959. Springer-Verlag, Berlijn-Göttingen-Heidelberg. Prijs in Nederland *f* 67.50.

In het in 1935 verschenen boek van Frey–Wyssling, "Die Stoffausscheidung der höheren Pflanzen", werd in het eerste gedeelte de celwand behandeld als uitscheidingsproduct van het protoplasma. Niet alleen het materiaal van de eigenlijke celwand, maar ook secundaire incrustaties (lignine) en afzettingen in en op de celwand (slijm, gom, was, suberine) werden beschreven, wat hun chemische eigenschappen, rangschikking en structuur betreft. Sedertdien is, in de eerste plaats als resultaat van de electronen-microscopie, de kennis op dit gebied zo toegenomen, dat een herbewerking van deze hoofdstukken leidde tot een zelfstandig boekwerk van 327 bladzijden (+ 28 bladzijden literatuur-opgave), toegelicht met 188 figuren, waaronder een reeks fraaie electronen-microscopische opnamen.

In dit voortreffelijke werk werden niet alleen resultaten verwerkt, verkregen met behulp van nieuwe methoden, maar ook aan de klassieke methoden van onderzoek van sub-microscopische structuren, o.a. met behulp van het polarisatie-microscoop (dubbele breking, dichroïsme), en aan de daarmee bereikte resultaten werd terecht zeer veel aandacht besteed. V. J. K.

PALYNOLOGIE - Bibliographie. Service d'information géologique du Bureau de Recherches géologiques, géophysiques et minières. 74, Rue de la Fédération. Paris-XV (France). Publié avec l'aide du Centre National de la Recherche Scientifique. Numéro: 3, janvier 1959, pp. 132. Prix 500 Francs.

The third volume of this annual report appeared promptly at the beginning of the new year. Contents: new list of names and addresses of palynologists (p. 5–34), bibliography containing the list of papers in the field of palynology published in 1958 or before if omitted in the previous volumes (p. 37–89), an index to the literature arranged according to the stratigraphy (p. 93–103), an index to the literature in geographical arrangement (p. 104–114), and an index to the literature arranged according to palynological topics (p. 115–131). F. P. J.

FLORA NEERLANDICA, issued by the Koninklijke Nederlandse Botanische Vereniging (Royal Botanical Society of the Netherlands), vol. 1, pt. 5. Orchidaceae by Dr. P. Vermeulen. Amsterdam 1958, pp. 127. Dfl. 15.—.

In accordance with the original intention of the Flora Neerlandica, Dr. Vermeulen gives in this issue an elaborate description of all species and forms of *Orchidaceae* which are known from the Netherlands.

The genus *Dactylorchis* especially has been treated thoroughly, and its infraspecific taxa are discussed in great detail. Vermeulen in 1947 raised this group to generic rank after it had been proposed as a subgenus by Klinge and others. In older Dutch floras, three species were distinguished, namely *Orchis maculata*, *O. latifolia*, and *O. incarnata*. The distinction between these species, however, caused great difficulties among floristic workers. There was also a continuing controversy between the German, Scandinavian, and British specialists about the taxonomy and nomenclature of the forms native in those areas.

After studying for many years the descriptions, living material, and herbarium collections from all over Europe, Vermeulen has arrived at sharp diagnoses of all forms native to the Netherlands, and has arranged these under six species.

A very important part of the work consists of distributional and ecological data, edited authoritatively by Dr. V. Westhoff. J. Hs.

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THE SPECTRAL DEPENDENCE OF FLOWERING AND ELONGATION [1]

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(*received March 17th, 1959*)

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ABSTRACT

Experiments with *Salvia occidentalis* (SDP) and *Hyoscyamus niger* (LDP) demonstrated that at least two photoperiodic reactions are involved in the process leading to a long-day effect. The main-light-period reaction is more sensitive to near infra-red and blue light than to red or green light. The effect of near infra-red and blue light can be antagonized by red light. The nightbreak reaction, promoted by red light, is nullified by a relatively short exposure to near infra-red or blue light.

Experiments with various plant species on the elongation of internodes have shown that at relatively low intensities red light is more inhibitive than blue light. At relatively high intensities blue light is the most inhibiting spectral region. The inhibiting effect of red light on the elongation of hypocotyls of light-grown gherkin seedlings is antagonized by a subsequent exposure to near infra-red or blue light. The inhibiting effect of red light on the hypocotyl of dark-grown gherkin seedlings is much more pronounced when the seedlings are pre-irradiated with white or blue light.

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[1] Thesis of the State University Utrecht.

1. INTRODUCTION

1.1 General

The subject of this investigation concerns two aspects of the influence of light of different spectral regions on plant development, 1° the response of the internode elongation and 2° the flowering response of photoperiodically sensitive plants.

Although the ultimate results are different, both processes have in common the same photoreaction, as the effect of an exposure to red light can be reversibly antagonized by an exposure to near infra-red radiation. The result of a treatment with red and near infra-red radiation, alternately given, is determined by the last radiation.

This antagonism between red and near infra-red was first of all reported to control seed germination (Borthwick *et al.* 1952*a*, 1954; Toole *et al.* 1955; Jones *et al.* 1956). Subsequently it was reported to regulate various other processes too, such as the flowering of photoperiodically sensitive plants (Borthwick *et al.* 1952*b*; Downs 1956), auxin induced growth of *Avena*-coleoptile sections (Liverman *et al.* 1953), pigment formation in the cuticle of tomato fruits (Piringer *et al.* 1954), internode elongation of both dark-grown seedlings (Downs 1955) and light-grown plants (Hendricks *et al.* 1956; Downs *et al.* 1957), leaf expansion of dark-grown seedlings (Downs 1955; Livermann *et al.* 1953, 1955), germination of fern spores (Mohr 1956), opening of the plumular hook of dark-grown bean seedlings (Klein *et al.* 1956), formation of protochlorophyll (Withrow *et al.* 1956), anthocyanin formation (Siegelman *et al.* 1957; Mohr 1957), frond multiplication of dark-grown Lemna (Hillman 1957), indole-acetic-acid oxidase activity (Hillman *et al.* 1957), the endogenous diurnal rhythm (Loercher 1958) and the tactic movement of chloroplasts (Haupt 1958). Thus it is obvious that this photochemical reaction is involved in different processes of plant development.

1.2 Photoperiodism

In many plants the initiation of flower buds depends on daylength (photoperiodism). In short days (i.e. long dark periods) flower buds are initiated in short-day plants (SDP); long-day plants (LDP), however, remain vegetative. When the plants are exposed to long days (i.e. short dark periods), flower initiation is prevented in short-day plants but induced in long-day plants. Not in all photoperiodically sensitive plants is the photoperiodic response an absolutely qualitative one. In some species a quantitative response is obtained: flowering is only accelerated by a special daylength.

A long-day effect can also be obtained either by extending a short day (main light period) with several hours of light at a relatively low intensity level (supplementary light) or by interrupting the corresponding long dark period with a relatively short irradiation (night-break). This effect of a night interruption makes it obvious that the photoperiodic response depends on a reaction in the long dark period.

As HAMNER (1940) has shown, however, the influence of the main light period may not be neglected.

A. *Influence of light during the dark period*

For a supplemental light treatment red light is especially effective for prolonging a short day (RASUMOV 1933; WITHROW *et al.* 1936*a*, 1936*b*, 1940; WASSINK *et al.* 1950, 1951; STOLWIJK 1952, 1954; KÖNITZ 1958).

The reaction on supplemental light therefore has the same action spectrum as the nightbreak reaction of both short-day and long-day plants (PARKER *et al.* 1946, 1950; BORTHWICK *et al.* 1948). It has been shown that radiation of the whole visible spectrum is effective provided that sufficient energy is given. A maximum of activity was found in the red region, a minimum in the green part and a second, less effective, maximum in the blue-violet region of the visible spectrum.

A reversible antagonism between red and near infra-red radiation has been found in photoperiodism. The long-day effect of a nightbreak with red light can be nullified by a following irradiation with near infra-red (BORTHWICK *et al.* 1952*b*). This antagonizing effect of near infra-red decreases or is completely absent if either a period of darkness between the red and the near infra-red is given for too long a time or if the irradiation time of the near infra-red treatment increases (DOWNS *et al.* 1956, CATHEY *et al.* 1957).

B. *Influence of the main light period*

The flowering response of *Xanthium pennsylvanicum* (SDP) does not depend only on the length of the dark period (HAMNER 1940) but also on the light intensity of the photoperiod. One long dark period induces flowering provided that it is preceded by a light period of high intensity.

KÖNITZ (1958) found that the flower-initiating effect of a short-day treatment on *Chenopodium amaranticolor* (SDP) was inhibited when the light period was interrupted with near infra-red radiation. This inhibiting effect of near infra-red radiation could be reversed by a following exposure to red light.

WALLRABE (1944) showed that a short-day treatment of *Kalanchoë blossfeldiana* (SDP) in blue light is more effective than the same treatment in red light; in green light no flower initiation occurred at all. In preliminary experiments with *Kalanchoë* and some other plant species MEIJER *et al.* (1957) were unable to confirm these results. Even in green light a short-day effect was obtained.

In long-day experiments in white light with the short-day plants *Perilla* (DE ZEEUW 1953) and *Salvia occidentalis* (MEIJER 1957*a*), a short-day effect (i.e. flower initiation) was obtained when the light intensity was sufficiently low.

In some cases the influence of the light quality of the photoperiod on the effect of a long-day treatment was studied. When *Hyoscyamus niger* (LDP) was grown in light of different spectral regions no long-day effect was obtained when the long-day treatment was given in yellow or green light. In red light, flower initiation was very much retarded as compared with the flowering response to a long-day treatment in blue, violet or red + near infra-red radiation (Stolwijk *et al.* 1955). As in these experiments the violet and blue light were contaminated with near infra-red it might be possible that only the near infra-red region was responsible for this effect. Currey *et al.* (1956), however, obtained the same effect in a long-day treatment in blue light without a near infra-red contamination.

This long-day activity of the violet-blue and the near infra-red regions appears quite remarkable, the more so as Stolwijk *et al.* (1955) confirmed the results of Parker *et al.* (1950) that red light —given as an interruption of a long dark period—is the most effective spectral region for obtaining a long-day effect. Similar results have been obtained in experiments with *Salvia occidentalis* (SDP) and some other plants (Meijer 1957*a*, 1957*b*).

From the results of these long-day experiments in coloured light one cannot determine whether the photoperiodic response was influenced during the main light period or during the supplemental light period. In nightbreak experiments with *Salvia* (SDP) and *Hyoscyamus* (LDP) it was shown that the long-day effect of an interruption of the long dark period with red light depends on the light quality of the main light period too (Meijer *et al.* 1957). A night interruption was only effective after a main light period in blue light; after a main light period in red or green light a nightbreak failed to induce a long-day effect.

It therefore seems obvious that in order to obtain a long-day effect at least three different reactions must take place: 1° a minimum rate of photosynthesis, 2° a specific main-light-period reaction and 3° a supplemental-light or nightbreak reaction. In this paper evidence is given in support of the assumption that whether a long-day effect is obtained or not depends on at least two photoperiodic reactions and not on the absolute duration of the photoperiod.

1.3 Elongation

In literature two opposite views exist about the influence of light of different spectral regions on the elongation of internodes:

1°. the blue part of the spectrum has the greatest inhibiting effect;
2°. red light is much more active in inhibiting the elongation than blue light.

Koningsberger (1922), studying "light growth reactions", reported that a brief exposure to blue light of an intensity of 2 erg/cm^2/sec was sufficient to retard temporarily the growth of Avena coleoptiles. Light of longer wave-length regions induced this effect only at much higher light intensities. Moreover the retardation due to blue light lasted longer than the retardation caused by an exposure to red light. The action spectrum of phototropism (e.g. Galston *et al.* 1949) also supports the conclusion of many investigators that blue light is the most active part of the spectrum in inhibiting the elongation of internodes (e.g. POPP 1926; ROODENBURG 1940; STOLWIJK 1954). FUNKE (1944) even concluded "that the red part of the spectrum acts like darkness" as far as the formative effect of light is concerned.

This conclusion, however, is not in agreement with the results of many other investigators who found that blue light was less effective then red light (e.g. DU BUY *et al.* 1930; WENT 1941; WITHROW 1941; WEINTRAUB *et al.* 1947; PARKER *et al.* 1949). This discrepancy could possibly be due to differences in the experimental methods e.g. to impurities of the spectral regions used, to the pretreatment of the plant material, to the light intensity or to differences between plant species.

A. *Light purity*

In some experiments plants were grown in day-light from which different short wave-length regions were eliminated by filters. POPP (1926) and SHIRLEY (1929) found that a lack of blue light caused an increase in internode elongation.

ROODENBURG (1940) using different gas discharge lamps, came to the same conclusion. ÅBERG (1943), however, found that the internodes of tomato plants in mercury light ("blue") were much more elongated than in neon or sodium light (respectively "red" and "yellow"). VAN DER VEEN (1950) used the light of coloured fluorescent lamps, which were coated with different monophosphors. Although he did not purify this coloured light the same results were obtained as with light obtained from fluorescent lamps and filtered by suitable filters (WASSINK *et al.* 1952; STOLWIJK 1954). Short internodes are formed in light of the blue-violet region, whereas in the longer wave-length regions internodes show a marked elongation. This was confirmed with several plant species by VINCE (1956, — *et al.* 1957) and MEIJER (1957*b*).

Nevertheless it was found that a contamination of a spectral region with light of other wave lengths can have a pronounced influence. MEIJER (1957*a*) compared *Salvia occidentalis* plants grown in blue light and in blue light + near infra-red. This light was obtained from blue fluorescent lamps purified by two different blue filters. One filter transmitted only the short wave-length region, the other one transmitted also the near infra-red ($\lambda > 7000$ Å). As the elongation of internodes was markedly increased in blue light + near infra-red as compared to pure blue light it is obvious that even a contamination with small amounts of near infra-red emitted by the fluorescent lamp should not be neglected. It was also shown that an addition of near infra-red radiation to blue or green light resulted in an increased elongation (MEIJER 1957*b*).

ROODENBURG (1940) was probably the first to ascribe to near infra-red an elongating effect. This effect has been definitely demonstrated by WASSINK *et al.* (1951), STOLWIJK (1954), DOWNS (1955, — *et al.* 1957) and HENDRICKS *et al.* (1956). The elongating effect of near infra-red radiation can be reversed by red light (STOLWIJK 1954; DOWNS 1955; — *et al.* 1957).

It has been found that the elongating effect of blue light, reported by Wassink *et al.* (1951) and Stolwijk (1954) must have been due to a contamination with near infra-red and not to the blue region itself (Wassink *et al.* 1957; Meijer 1957*a*). Nevertheless Meijer (1957*b*, 1958*a*) obtained in some cases a stimulation of the elongation by pure blue-light.

B. *Pretreatment*

The varying results could also be due to the pretreatment of the plant material. Whether dark-grown seedlings have been used in the experiments or green plants previously raised in light might have an influence on the result.

Etiolated or dark-grown plants are characterized by a strong elongation of the internodes, the development of small leaves (as far as Dicotyledons are concerned) and usually a lack of chlorophyll (as far as Angiospermae are concerned). Relatively small amounts of light are enough to prevent etiolation: the elongation of the internodes decreases whereas the leaf size increases.

When dark-grown plants are used the material is not yet influenced by white light before the experiments start. With light-grown plants one will not find a primary effect on the elongation but a secondary one, i.e. on the inhibited elongation.

This difference in reaction has been clearly demonstrated by the effect of an irradiation with near infra-red or blue light. Near infra-red has an inhibiting effect on the elongation of dark-grown seedlings (Withrow 1941; De Lint 1957). On plants previously irradiated with white light (Downs *et al.* 1957) or light of different spectral regions (De Lint 1957) near infra-red has an elongating effect. Similar effects have been reported for blue light (Meijer 1957*b*, 1958*a*).

Wassink *et al.* (1956) stated in a review that "in etiolated plant material the red spectral region is most effective in this respect (i.e. in the inhibition of elongation), whereas in light-grown plants and at high light intensities the violet-blue region of the spectrum is especially effective".

This statement is not always valid. It was shown that several plant species, previously raised in white fluorescent light, acquired much longer hypocotyls in blue than in red light. (Meijer 1957*b*, 1958*a*). Again Vince *et al.* (1956, 1957) obtained longer internodes with *Pisum* and *Calendula* in blue light than in red light. In her experiments with *Pisum* this author used "dark-grown" seedlings as the plants were exposed to light of the different wave-length regions directly after sowing. For *Calendula* it is not reported whether the plants were raised in white light before the treatment or not. We were able, however, to confirm this result with light-grown *Calendula* plants.

C. *Light intensity*

According to Åberg (1943) it seems possible that the light intensity might influence the results. He postulated that at low light intensities the red region is the most active, whereas at high light intensities the blue-violet region is the most effective part of the visible spectrum for inhibiting the elongation. Although several investigators have compared light of different energy levels, this assumption has not been confirmed (WITHROW 1941; VINCE 1956, — *et al.* 1957).

D. *Plant species*

As different plant species did not give a similar reaction when grown under exactly the same conditions it was concluded that the response to light of different spectral regions depends more on differences in plant species than on the experimental method (VINCE 1956, — *et al.* 1957; MEIJER 1957*b*). In this paper it will be shown that this conclusion is rather premature and that plants of the same species react in a different way depending on the light intensities used.

2. MATERIAL AND METHODS

Various plants sensitive to daylength were used in the experiments on photoperiodism. *Sinapis alba*, *Arabidopsis thaliana* (3 strains), *Nasturtium palustre*, *Chrysanthemum parthenium*, *Hyoscyamus niger* and *Petunia hybr.* all long-day plants, were sown and raised in a glasshouse under short-day conditions and afterwards subjected to a treatment which was continued until flower buds were macroscopically visible. *Salvia occidentalis*, *Kalanchoë blossfeldiana*, *Euphorbia pulcherrima* and *Xanthium pennsylvanicum*, all short-day plants, were propagated by means of cuttings, the use of clones giving very homogeneous material. These plants were grown under long-day conditions, which prevented flower initiation. After the treatment had lasted sufficiently long to induce flower initiation when exposed to short days, the plants were transferred to the glasshouse under conditions of non-inductive daylength.

At the beginning of the treatment the plants were selected for uniformity. A control group stayed under conditions of non-flower-inducing daylength and was compared with the treated plants to ascertain that flower initiation had not already been induced before the treatment started. The youngest developed leaf was marked at the beginning of an experiment and after the experiment was discontinued all the newly developed leaves or pairs of leaves were counted. Plants were considered to be vegetative when this number of leaves of the non-generative plants was larger than the number of leaves of the generative plants, developed before flower buds were initiated. Moreover the plants were dissected.

In this paper the influence of the light quality on the photoperiodic response is studied with special reference to the long-day effect on *Salvia occidentalis*. A long-day treatment prevents flower initiation in short-day plants and promotes this process in long-day plants. For this reason the results obtained with long-day plants and short-day plants are compared in terms of short-day effect or long-day effect and not in terms of flowering or non-flowering response.

For the sake of convenience the length of a supplemental-light period is given in number of hours, the duration of a nightbreak in number of minutes followed by an apostrophe.

The experiments with *Salvia occidentalis* are described in 3.1–3.1.3. The results obtained from experiments with other plants are given in 3.1.4.

The influence of light of different spectral regions on elongation was studied on various plant species: *Solanum lycopersicum* (tomato, "Victory"), *Hyoscyamus niger*, *Sinapis alba*, *Cucumis sativus* (gherkin, "Venlose niet plekkers"), *Phaseolus vulgaris* (bean, "Vroege Wagenaar") and *Mirabilis jalapa*.

Two different methods were used.

1. The seeds were left to germinate and the seedlings raised in white light before the treatment with coloured light started ("light-grown plants").

2. The seedlings were not previously exposed to white light but were raised from seed in the light cabinets. Although these seedlings were exposed to coloured light, they will be referred to as "dark-grown seedlings" in contrast with the "light-grown seedlings" which had received white light prior to the treatment in the light cabinets.

In the experiments with "light-grown plants" 7–10 plants were used per treatment. The seeds were sown in seed pans and the seedlings potted after some time. As soon as the plants resumed growth, they were selected and subjected to the treatment.

"Dark-grown seedlings" were sown in pots about 20–25 seeds per pot, except beans of which 7 seeds were used per pot. Some days after germination the seedlings were selected for uniformity. The most vigorous seedlings, which had germinated early, and the seeds which had just started to germinate or had not germinated yet were discarded. The length of internodes was measured each 2–4 days until the organ showed to have finished elongation. The results of these experiments are given in 3.2.

The light cabinets in which the plants were exposed to light of different spectral regions have been described before (VAN DER VEEN *et al.* 1958). Fluorescent lamps (80 Watt) are mounted to the top and at two sides. In this way high light intensities and an equal light distribution are obtained. In those cases in which low light intensities were wanted, either cages of gauze were used or a number of lamps was switched off. In the experiments with supplementary light (3.1.2) and with "very low intensities" (3.2) only some of the lamps mounted to the top were switched on.

The lamps also provided the heat; the temperature was kept constant by means of a water-cooling system controlled by a thermostat. The day temperature was kept at 22° C. When the lamps were switched off the temperature decreased to that of the surrounding room, viz. 17° C. When only some of the lamps were used (see above) it was necessary to use heating elements also controlled by a thermostat. In this way it was possible to keep the temperature constant between 21.5° and 22.5° C.

The visible radiation was obtained from different types of fluorescent lamps ("TL") with suitable filters of "Plexiglas" (Röhm & Haas). The characteristics of the light conditions have been given extensively in a previous paper (MEIJER 1957*a*). "TL" 33 lamps were used to provide "white" light. Red light was obtained in the wave length region of $\lambda = 6000$–7000 Å, although $\pm 2\,\%$ radiation was emitted in the infra-red region ($\lambda > 7000$ Å). Green light was more or less restricted to the region of $\lambda = 5000$–6000 Å. Blue light, without a contamination of red or near infra-red, consisted of radiation in the region of $\lambda = 4000$–5300 Å. Less than $1\,\%$ was obtained in the ultra-violet region ($\lambda < 4000$ Å). Near infra-red (= far red) radiation of the wavelength region of $\lambda > 7000$ Å was obtained from either incandescent lamps or neon lamps. In both cases the radiation was filtered by a combination of "Plexiglas" filters which transmitted radiation with $\lambda > 7000$ Å. To avoid too much radiation with $\lambda > 10000$ Å—which is known to have only a temperature effect—a water filter of 2 cm thickness was used. The intensity is given for the region of $\lambda = 7000$–8000 Å. As incandescent light shows a continuous spectrum and neon light a line spectrum, the intensities of near infra-red radiation obtained from these two types of lamp cannot be compared. Unless stated otherwise, near infra-red radiation was obtained from the incandescent lamps.

The light intensities are given in μW/cm^2. Foot candles or lux cannot be used because these units depend on the sensitivity of the human eye. Radiation was measured with a photocell. As the sensitivity of a photocell changes with the wavelength, it was calibrated against a thermopile for each combination of lamps and filter(s). The light intensities were measured as incident on a horizontal surface.

3. EXPERIMENTAL RESULTS AND DISCUSSION

3.1 PHOTOPERIODISM

Preliminary experiments in white light have shown that *Salvia occidentalis* is an obligate short-day plant. Specimens irradiated during 16 hours per day remained completely vegetative. When the irradiation was restricted to 10 hours of light per day, flowering was initiated.

The degree of flower initiation depends on the number of short days (10 hours of light per day) to which plants are exposed. It was found that a short-day treatment during 10 days or less was without effect. When the treatment lasted at least 16 days flowering was initiated and in the following long days a normal inflorescence bud was formed. A short-day treatment of 10 to 16 days resulted in a slight flower induction. In the long days which followed only some bractlike leaves developed and the vegetative growth of the growing points was resumed. In the following experiments the treatment lasted at least 21 days to make sure that flowering was sufficiently induced.

The critical daylength was determined by exposing plants to white fluorescent light during photoperiods of different lengths. It was found that this critical daylength was between 13 and 15 hours of light per day (Table 1). In this experiment the light intensity during the whole photoperiod was 2900 $\mu W/cm^2$. The treatment lasted 26 days after which the plants were transferred to long-day conditions.

TABLE 1

The influence of the length of the photoperiod in white fluorescent light on the flowering response of *Salvia occidentalis*. Light intensity: 2900 $\mu W/cm^2$. Duration of the treatment 26 days. Number of plants per treatment 3. + = generative (short-day effect), — = vegetative (long-day effect). Observations 26 and 42 days after the beginning of the treatment.

Length of photoperiod in hrs per day	Condition of the growing point after:						Number of newly formed leaf pairs after 42 days					
	26 days			42 days			+			—		
9	+	+	+	+	+	+	4	4	5			
11	+	+	+	+	+	+	5	5	5			
13	—	—	—	—	+	+	6	6	6			
15	—	—	—	—	—	—				> 9	> 9	> 9
16	—			—	—	—				> 9	> 9	> 10

The last observations were made 42 days after the beginning of the treatment. In the subsequent long-day experiments the photoperiod was 16 hours of light per day, this being of sufficient length for obtaining a long-day effect, i.e. the prevention of flower initiation.

3.1.1 LONG-DAY TREATMENT

a. *White light*

It appeared that the critical daylength also depends on the light intensity of the photoperiod, irradiation during 16 hours of light per day not always having a long-day effect on the flowering response of *Salvia occidentalis*. In Table 2 the results of two experiments are presented. The plants were grown in 16 hours of white fluorescent light per day at different intensities. The last observations in Experiment I were made after the treatment had lasted 39 days; in Experiment II, 39 days after the beginning of the treatment which lasted 25 days. It was found that flowering was initiated if the light intensity was sufficiently low, despite the fact the plants were exposed to long days.

TABLE 2

The influence of the light intensity of the photoperiod on the flowering response to a long-day treatment in 16 hrs white fluorescent light per day. Experiment I: 3 plants per treatment, observed after a treatment of 39 days. Experiment II: 6 plants per treatment, observed 39 days after the beginning of a treatment of 26 days. + = generative (short-day effect); — = vegetative (long-day effect), (—) = vegetative.

Light intensity in $\mu W/cm^2$	85	250	400	660	850	1250	2500
Experiment I		+			—		—
Experiment II	(—)		+	+			

At an intensity of 850 $\mu W/cm^2$ or higher a long-day effect was obtained whereas at intensities from 250 to 660 $\mu W/cm^2$ flower initiation was not prevented. In light of an intensity of 85 $\mu W/cm^2$ no flower initiation occurred, the growth being quite poor, only two leaf pairs developing during the treatment. At higher intensities this number was 4 or 5.

b. *Coloured light*

To investigate which spectral region is the most active in obtaining a long-day effect, the plants were exposed to long days in red, green or blue light.

In a number of experiments 16 hours of red, green blue or white light were used per day. Gauze filters enabled three or four different light intensities to be compared in each experiment. The results are collected in Table 3. The duration of the treatment varied for the various experiments but was never less than 26 days.

TABLE 3

The influence of the light quality on the photoperiodic effect of a long-day treatment of 16 hrs light per day. + = generative (short-day effect); — = vegetative (long-day effect); (—) = vegetative.

Irradiation in hrs per day	Light intensity in $\mu W/cm^2$			
	0	500	1000	1500
16 Red	(–) + + –	–	–	–
16 Green	(–) + +	+	+	–
16 Blue	(–) – –	– – –		
16 White	(–) + +	+ –	–	

It is obvious that in a long-day treatment light from each region of the visible spectrum is active in causing a long-day effect provided that the light intensity is sufficiently high. Blue light (16B), however, showed to be the most active type of light, followed by red light (16R). Green light (16G) is only slightly active in this respect, rather high intensities being necessary for obtaining a long-day effect by means of a long-day treatment of 16 hours of light per day. At very low intensities (85 $\mu W/cm^2$) no flower initiation occurred during any light treatment. This prevention of flower initiation may be due to reasons other than a long-day effect of the 16-hour light treatment as it was found that at low light intensities even a short-day treatment fails to initiate flower buds.

Although irradiation with 16 hours of red light per day (16R) at an intensity of 370 $\mu W/cm^2$ did not prevent flower initiation (see Table 3), this short-day effect is different from the effect of a short-day treatment (10 hours of light per day) in red light of the same intensity. In consequence of the short-day treatment (10R), flowering was initiated as soon as 5 new leaf pairs had developed. After the long-day treatment (16R), however, the number of leaf pairs developed before flower buds were initiated was eight and the flower buds became later visible too. So there still was some indication of an inhibition of flower initiation (long-day effect) by the long-day treatment (16R) as compared to the response to a short-day treatment (10R) in red light. At an intensity of 260 $\mu W/cm^2$ a long-day treatment in red light showed hardly any long-day effect as the appearance of the flower buds was scarcely delayed; the average number of newly formed leaf pairs being 6.3.

A long-day treatment in green light (16G) at an intensity of 500 $\mu W/cm^2$ did not cause any long-day effect. Flower buds were initiated after 5 newly formed pairs of leaves. At 900 $\mu W/cm^2$ a slight retardation was found; a small increase could be observed in the number of leaf pairs formed prior to the first flower bud, viz. 6.5.

c. *Near infra-red radiation*

The influence of near infra-red radiation on the photoperiodic effect of a long-day treatment in coloured light was studied in the following experiments.

The plants were exposed to red, green or blue light with and without an addition of near infra-red during 16 hours per day (16R, 16RIR, 16G, 16GIR, 16B, 16BIR). The light intensity of the visible radiation was 300 $\mu W/cm^2$. It was found (see Table 3) that under these conditions a long-day treatment in red or green light does not prevent flowering i.e. no long-day effect is obtained. Those plants which were exposed to near infra-red radiation were unilaterally irradiated, this method permitting intensity ranges up to 130 $\mu W/cm^2$ to be studied. In all 9 different intensities were used. At each intensity only one plant was used to avoid one plant shading the other. At the lowest intensity, 3 plants were used. The number of control plants was 10. After this treatment which lasted 30 days, the plants were transferred to long-day conditions. The last observations were made after 70 days. The results are shown in table 4 (Plate 1–a).

TABLE 4

The influence of near infra-red radiation on the photoperiodic effect of a long-day treatment (16 hrs per day) in red, green or blue light (300 $\mu W/cm^2$). Duration of the treatment 30 days. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 70 days.

Light treatment 16 hrs per day	Intensity of I R in $\mu W/cm^2$		
	0 – 50	50 – 100	100 – 150
Red + I R	+ +++ +	− − −	− −
Green + I R	+ +++ −	− − −	− −
Blue + I R	− −−− −	− − −	− −

Near infra-red radiation used simultaneously did not influence the effect of a long-day treatment in blue light (16B, 16BIR); all plants remained completely vegetative. After 70 days the average number of newly formed leaf pairs of plants treated with 16B and 16BIR was 10.8 and 9.1 respectively.

Addition of near infra-red to green light (16GIR) was found to be very effective in causing a long-day effect since it prevented flowering, initiated in long-days in green light (16G). In 16G the average number of new leaf pairs developed before flower initiation occurred was 5.9. In 16GIR, with a near infra-red intensity of 45 μW/cm^2 or higher, plants remained vegetative and the number of newly formed leaf pairs was more than 9. Near infra-red of lower intensities did not prevent flower initiation but at most retarded it a little. With increasing intensities from 0–35 μW/cm^2 the number of newly formed leaf pairs was 6, 6, 6 and 7, respectively.

In long days in red light (16R) flower initiation occurred; it was, however, retarded as compared with plants grown in green light (16G). The average number of leaf pairs developed before flower initiation occurred was 7.7. Addition of near infra-red (16RIR) of a higher intensity than 50 μW/cm^2 prevented flowering (long-day effect); after 70 days more than 10 pairs of leaves were developed and still no sign of flower initiation could be observed. At lower intensities of near infra-red, flower initiation was not prevented but more or less retarded as compared with plants grown in red light without any addition of near infra-red (16R). With the near infra-red intensity increasing from 0–45 μW/cm^2 the number of leaf pairs developed before flower buds were initiated was 7.7, 9, 10, 10 and 10, respectively.

In experiments with 16 hours green + near infra-red per day, in which the number of different intensities of near infra-red investigated was reduced to 3 or 4, it was possible to treat simultaneously 3 or 4 plants at each intensity. Probably the effect of one plant shading the other was even better avoided under these conditions since it was found that in this case even 30 μW/cm^2 near infra-red radiation were effective in producing a long-day effect.

Similar results were obtained when the intensity of the visible radiation was increased. However, at an intensity of e.g. 510 μW/cm^2, already an irradiation with red light during 16 hours per day was sufficient for obtaining a long-day effect, flower initiation then being prevented. Addition of near infra-red radiation (16RIR) did not counteract this long-day activity of the red light.

In preliminary experiments the plants were exposed to 16 hours of green light per day (16G) to which near infra-red was added during

a) the last 8 hours (8G 8GIR)
b) the first 8 hours (8GIR 8G) or
c) the total photoperiod (16GIR)

It was found that a long-day treatment with 16 hours of green light already resulted in a long-day effect when only during part of the photoperiod near infra-red was added. The results of one of these experiments are given in Table 5.

The intensity of the green light was 400 μW/cm^2 and of the near infra-red radiation 160 μW/cm^2. The duration of the treatment was 25 days after which the plants were transferred to long-day conditions. The results show that it made no difference whether the near infra-red was added during the first or the second 8 hours of the photoperiod.

TABLE 5

The influence of an addition of near infra-red (200 μW/cm^2) on the photoperiodic effect of a long day treatment (16 hrs per day) in green light (400 μW/cm^2). G = green, IR = near infra-red. Duration of the treatment 25 days. Number of plants per treatment 3. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 48 days.

Light treatment		Condition of the growing point
8 hrs	8 hrs	
8G	8G	+ + +
8G	8GIR	— — —
8GIR	8G	— — —
8GIR	8GIR	— — —

If, however, the duration of the near infra-red irradiation was shortened its effect was clearly influenced by the moment at which this radiation was added. In the following experiment plants were exposed to 2, 4 or 8 hours of green + near infra-red, either followed or preceded by 14, 12 or 8 hours of green light (2GIR 14G, 4GIR 12G . . . 14G 2GIR) respectively. The intensity of the green light was 370 μW/cm^2 and of the near infra-red 130 μW/cm^2. The treatment lasted 25 days, after which the plants were exposed to long days. The results are given in Table 6.

TABLE 6

The influence of near infra-red (130 μW/cm^2) on the photoperiodic effect of a long-day treatment (16 hrs per day) in green light (370 μW/cm^2). Duration of the treatment 25 days. Number of plants per treatment 3. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 42 days.

Light treatment in hrs per day		Condition of the growing point
2GIR	14G	+ + +
4GIR	12G	+ + —
8GIR	8G	— — —
8G	8GIR	— — —
12G	4GIR	— — —
14G	2GIR	— — —

The plants which remained vegetative showed 10 or 11 pairs of leaves, developed in the 42 days after the beginning of the treatment. The generative plants stopped leaf formation after 6 or 7 pairs of leaves and subsequently initiated flower buds.

It is obvious from these results that an addition of near-infra-red during 4 hours per day contributed more towards obtaining a long-day effect when given at the end (12G 4GIR) than at the beginning of the 16-hour green light period, (4GIR 12G). Added at the end of the daily light period, 2 hours of near infra-red (14G 2GIR) were still effective in preventing flower initiation, but they were completely ineffective when given at the beginning of the light period (2GIR 14G).

In other experiments the near infra-red radiation was alternated with green light. In one of these experiments the intensity of the green light was 1200 μW/cm^2 and of the near infra-red (obtained from a neon lamp) 150 μW/cm^2. The daily irradiation with green light lasted 16 hours (16G). One hour of this green light was replaced by near infra-red which was given 0, 3, 6, 9, 12 or 15 hours after the beginning of the light period (1IR 15G, 3G 1IR 12G . . . 15G 1IR). The plants were subjected to this treatment during 25 days and afterwards transferred to long-day conditions. The last observations were made after 48 days; the results are presented in Table 7 (Plate 1–b).

TABLE 7

The influence of near infra-red (150 μW/cm^2) on the photoperiodic effect of a long-day treatment (16 hrs per day) in green light (1200 μW/cm^2). Duration of the treatment 25 days. Number of plants 3. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 48 days.

Light treatment in hrs per day			Condition of the growing point		
—	—	16G	+	+	+
—	1IR	15G	+	+	+
3G	1IR	12G	+	—	—
6G	1IR	9G	—	—	—
9G	1IR	6G	+	+	+
12G	1IR	3G	+	+	+
15G	1IR	—	—	—	—

The vegetative plants developed 10 to 11 new pairs of leaves in the 48 days after the beginning of the experiment. In the generative plants flower initiation occurred after about 6 pairs of new leaves had been formed.

It is clear that an irradiation with 1 hour of near infra-red is only effective in causing a long-day effect if it is preceded by a green light period of at least 3 hours (3G1 IR 12G). On the other hand such a preceding irradiation cannot be the only condition for obtaining a long-day effect. 9G 1IR 6G and 12G 1IR 3G did not have any long-day effect at all, although in these groups the near infra-red was preceded by even more than 3 hours of green light. Probably a second condition exists: light is also necessary in a period about 9 hours after the beginning of the irradiation with near infra-red. Those treatments which resulted in a long-day effect fulfilled both conditions viz. 15G 1IR, 6G 1IR 9G and 3G 1IR 12G (partly). When flowering was not prevented, either the first condition was not fulfilled viz. 1IR 15G, or the second condition viz. 9G 1IR 6G and 12G 1IR 3G.

d. *Antagonism*

It has been reported that the long-day effect of an interruption of a long night (= short day) with red light can be antagonized by a subsequent exposure to near infra-red radiation. The following experiments were carried out to investigate whether, conversely, the long-day effect of near infra-red and possibly also of blue radiation can be counteracted by a subsequent exposure to red light or not.

The plants were exposed to 15 hours of green light followed by

a) 1 hour of green light (16G)
b) 1 hour of green and ½ hour of red light (16G ½R)
c) 1 hour of near infra-red (15G 1IR) and
d) 1 hour of near infra-red and ½ hour of red light (15G 1IR ½R).

The intensity of both the green and the red light was 650 μW/cm^2. The near infra-red was obtained from a neon lamp with an intensity of 120 μW/cm^2. Each group consisted of 5 plants. After a treatment of 28 days the plants were transferred to long days. The results of this experiment are given in Table 8. (Plate 1–c).

TABLE 8

The antagonizing activity of red light (650 μW/cm^2) on the photoperiodic effect of near infra-red (120 μW/cm^2) given after a long day in green light (650 μW/cm^2). Duration of the treatment 28 days. Number of plants per treatment 5. + = generative (short-day effect), — = vegetative (long-day effect). Observations after 60 days.

Light treatment in hrs per day			Condition of the growing point				
15G	1G	—	+	+	+	+	+
15G	1G	½R	+	+	+	+	+
15G	1IR	—	—	—	—	—	—
15G	1IR	½R	+	+	+	+	+

It is obvious from these results that the long-day effect caused by 1 hour of near infra-red irradiation (15G 1IR) was nullified by a subsequent exposure to red light (15G 1IR ½R). This red light itself (16G ½R) did not influence the effect of a long-day treatment in green light (16G).

Similar experiments were carried out with blue light instead of near infra-red. In one of these experiments the intensity of the green light was 640 μW/cm^2 and that of both the blue and the red light 760 μW/cm^2. Each lot consisted of 6 plants. After the treatment which lasted 25 days the plants were kept in long-day conditions. The results presented in Table 9 (Plate 1–c) show that the long-day effect of blue light is completely comparable with the effect of near

TABLE 9

The antagonizing activity of red light (760 μW/cm^2) on the photoperiodic effect of blue light (760 μW/cm^2) given after a long day in green light (640 μW/cm^2). Duration of the treatment 25 days. Number of plants per treatment 6. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 70 days.

Light treatment in hrs per day			Condition of the growing point					
15G	1G	—	+	+	+	+	+	—
15G	—	1R	+	+	+	+	+	+
15G	1B	—	—	—	—	—	—	—
15G	1B	1R	+	+	+	+	+	—

infra-red radiation, since both can be antagonized by a subsequent exposure to red light.

From these experiments carried out in long days it can be concluded that blue and near infra-red radiation are the most active types of light in preventing flowering, i.e. for obtaining a long-day effect. Red light was much less effective whereas in green light only at relatively very high intensities a long-day effect could be obtained. In addition it became apparent that this long-day effect caused by blue or near infra-red radiation can be antagonized by a subsequent irradiation with red light.

3.1.2 SUPPLEMENTAL LIGHT TREATMENT

The results presented in the foregoing chapter, showing that blue and near infra-red are more active in causing a long-day effect than red or green light, are not in agreement with the results obtained with numerous plants from supplemental or nightbreak experiments, which have shown that red light is the most active type of light.

In a preliminary experiment with *Salvia occidentalis*, the plants were exposed to short days of 8 hours of white fluorescent light per day (main light period). The intensity was 2100 μW/cm². During the 8 hours after this main light period, the plants were

a) kept in darkness (8W) or irradiated with
b) red (8W 8r),
c) green (8W 8g) or
d) blue light (8W 8b) of different intensities.

All plants were kept in darkness for the remaining 8 hours per day. Each lot consisted of 5 plants. After a treatment of 28 days, plants were replaced in long-day conditions. The last observations were made after 52 days, the results are given in Table 10.

TABLE 10

The influence of the light quality on the photoperiodic effect of 8 hrs supplemental light (8r, 8g or 8b) given after a main light period (short day) of 8 hrs white fluorescent light per day (2100 μW/cm²). Duration of the treatment 28 days. 5 Plants per treatment. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 52 days.

Light treatment	Intensity of the supplemental light (r, g, b) in μW/cm²									
in hrs per day	0	50	65	85	250	325	415	500	650	830
8W	+									
8W 8r			+			—			—	
8W 8g				+			+			+
8W 8b		—			—			—		

The generative plants developed 5 or 6 pairs of leaves before initiating flower buds, the vegetative plants showed 7 or 8 newly formed pairs of leaves. As can be seen in Table 10, at lower intensities blue light is more active than red light in prolonging the short main light period, resulting in a long-day effect. At higher intensities, both blue and red light are effective.

According to the available literature, experiments on the influence of supplemental light and nightbreak light have always been carried out with main light periods (short days) in white light. This paper describes a number of experiments carried out to determine the influence of the quality of the light, used during this main light period on the photoperiodic effects of supplemental light and nightbreak light (see also 3.1.3).

First of all it was necessary to find out whether the light quality influences the photoperiodic effect of a short-day treatment, i.e. the initiation of flower buds. To this purpose plants were exposed daily to 10 hours of red, green or blue light with an intensity of about 900 μW/cm^2. These short-day treatments lasted 2, 4, 6, 8, 10, 12, 14 or 16 days after which the plants were transferred to long-days. A short-day treatment during 10 days or less in red or in blue light and during 8 days or less in green light was ineffective in inducing flower initiation. If the short-day treatment lasted longer, plants exposed to red, green or blue light became generative to the same extent, at the same time and after the formation of about the same number of leaves. Apparently under these experimental conditions, the photoperiodic effect of a short-day treatment did not depend on the light quality of the photoperiod but only on the duration of the short-day treatment.

In the following experiment the influence of the light quality of both the main light period and the supplemental light period on the photoperiodic effect is demonstrated. Plants were irradiated daily with 10 hours of red (10R), green (10G), green + near infra-red (10GIR) or blue light (10B). The intensity of the visible radiation was 450 μW/cm^2 and of the near infra-red added to green light 115 μW/cm^2. After this main light period 3 plants of each group were exposed for another 8 hours to supplemental light of low intensity in red (10R 8r etc.) or blue (10R 8b etc.). This supplemental light treatment was given at a low intensity of 160 μW/cm^2. To obtain this low intensity, the plants were only irradiated from above, using the lamps mounted to the top of the light cabinet. For this reason this low light intensity is not quite comparable with those applied during treatments in which plants were irradiated from three sides. The same procedure was followed in all other experiments with supplemental light. After a treatment of 30 days, the plants were kept in long-day conditions for another 35 days. The results are given in Table 11 (Plate 1–d).

The generative plants developed 4–6 pairs of leaves before initiating flower buds; the vegetative plants showed about 12 newly formed pairs of leaves after 65 days.

Supplemental light, whether 8 hours of red or 8 hours of blue used after a short-day period in green light (10G 8r, 10G 8b) did not cause any long-day effect. If, however, near infra-red radiation was used simultaneously with the green light (10GIR), 8 hours of red as well as 8 hours of blue supplemental light (10GIR 8r, 10GIR 8b) did produce a long-day effect.

TABLE 11

Photoperiodic effect of a supplemental irradiation with 8 hrs red or blue light (160 μW/cm^2) given after a main light period of 10 hrs red, green, green + infra-red or blue light (450 μW/cm^2). Intensity of near infra-red 115 μW/cm^2. Duration of the treatment 39 days. 3 Plants per treatment. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 65 days.

Main light period in hrs per day	Supplemental light period		
	8 hrs dark	8 hrs red	8 hrs blue
10R	+ + +	+ + +	+ — —
10G	+ + +	+ + +	+ + +
10GIR	+ + +	— — —	— — —
10B	+ + +	+ + +	— — —

After a main light period in blue light only a supplemental light treatment with blue light (10B 8b) caused a long-day effect; 8 hours of red light (10B 8r) did not prolong the short main light period.

After a short day in red light, 8 hours of supplemental red light (10R 8r) did not prevent flower initiation, supplemental blue light (10R 8b), however, did. The long-day effect obtained with 10R 8b was somewhat less pronounced than that obtained with 10B 8b. All the growing points, terminal or axillary, of the plants treated with 10B 8b remained completely vegetative, but the plants exposed to 10R 8b showed a generative tendency, one plant of this group developing 3 pairs of bractlike leaves after which normal vegetative growth was resumed; moreover, all the laterals of the plants of this group initiated flower buds.

In a similar experiment the main light period lasted only 8 hours and the intensity of the supplemental irradiation was only 95 μW/cm^2 in stead of 160 μW/cm^2 as in the foregoing experiment. The results of this experiment which lasted 30 days are collected in Table 12. The last observations were made 75 days after the beginning of the treatment. All plants which remained vegetative had developed about 15 new pairs of leaves, the generative plants initiated flowering after about 6–8 newly formed leaf pairs.

TABLE 12

Photoperiodic effect of a supplemental irradiation with 8 hrs red or blue light (95 μW/cm^2) given after a main light period of 8 hrs red, green, green + infra-red or blue light per day (470 μW/cm^2). Intensity of near infra-red: 115 μW/cm^2. Duration of the treatment 30 days. Number of plants per treatment 4. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 75 days.

Main light period in hrs per day	Supplemental light period		
	8 hrs dark	8 hrs red	8 hrs blue
8R	+ + + +	+ + + +	+ + + +
8G	+ + + +	+ + + +	+ + + +
8GIR	+ + + +	+ + — —	— — — —
8B	+ + + +	+ + + +	+ + + +

Under these conditions only a treatment with a main light period containing near infra-red radiation was active in producing a long-day effect and blue supplemental light (8GIR 8b) was found to be more active than red supplemental light (8GIR 8r).

Thus the results of the experiments carried out in long days are in agreement with those of the experiments with supplemental light after a short-day period, all results indicating that blue and near infra-red radiation are more active than red light in preventing flowering (long-day effect).

In a previous paper it has been reported that red nightbreak light is more active than blue light in preventing flowering of *Salvia occidentalis*. (MEIJER *et al.* 1957). To get some information about the difference between nightbreak light and supplemental light treatments, experiments were carried out comparing both types of treatment and the change-over from one into the other.

The plants were grown in 10 hours of red (10R) and 10 hours of blue light (10B) per day; the light intensity was 670 μW/cm^2. After this short main light period, separate groups of 3 plants were treated with

a) 8 hours of red (10R 8r, 10B 8r) or blue light (10R 8b, 10B 8b),
b) 4 hours of darkness followed by 4 hours of red (—4D 4r) or 4 hours of blue light (—4D 4b),
c) 6 hours of darkness followed by 2 hours of red (—6D 2r) or 2 hours of blue light (—6D 2b),
d) 7 hours of darkness followed by 1 hour of red (—7D 1r) or 1 hour of blue light (—7D 1b),
e) 7½ hours of darkness followed by ½ hour of red (—7½D ½r) or ½ hour of blue light (—7½D ½b) and
f) no supplemental light (10R and 10B).

All plants were kept in darkness for the remaining 6 hours per day. The intensity of the supplemental red and blue light was 185 μW/cm^2. After 26 days the treatment was discontinued and the plants were returned to long-day conditions. The last observations were made after 56 days, the results are given in Table 13 (Plate 2–e).

TABLE 13

Photoperiodic effect of blue and red light (185 μW/cm^2) given in an 8-hour period following after a main light period of 10 hrs red or blue light (670 μW/cm^2). Duration of the treatment 26 days. 3 Plants per treatment. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 56 days.

Main light period		10 hrs Red		10 hrs Blue	
Supplemental 8-hour period		red	blue	red	blue
hrs dark	hrs light				
0	8	+ + +*	— — —	+ + +	— — —
4	4	+ + +	+ + +	— — —	— — —
6	2	+ + +	+ + +	— — —	+ + +
7	1	+ + +	+ + +	— — —	+ + +
7½	½	+ + +	+ + +	— — —	+ + +
8	0	+ + +		+ + +	

*SEE TEXT.

The plants exposed to 10R or 10R 8r did not remain vegetative, but a treatment with 10R 8b prevented flower initiation. Although 10R 8r did not prevent flower initiation, yet this process was somewhat retarded (8 pairs of leaves formed before flower buds were initiated) when compared to the other groups of generative plants (4–6 pairs of leaves developed prior to flower initiation).

All plants, receiving a few hours of darkness between the main light period in blue light (10B) and the additional red light (– r) remained vegetative (10B 4D 4r . . . 10B 7½D ½r). If the red light, however, immediately followed the main light period (10B 8r) no long-day effect was obtained.

When blue light (—b) was given in the 8-hour period after 10B, a long-day effect was only obtained with 4 or 8 hours of additional blue light (10B 4D 4b, 10B 8b); less than 4 hours of blue light (10B 6D 2b, . . . 10B 7½D ½b) were not effective in preventing flower initiation.

It is obvious that as far as 10B 8r is concerned, the ineffectiveness of red supplemental light in causing a long-day effect cannot be due to an inactivity of the red light itself as 4 hours of red (10B 4D 4r) or less succeeded in preventing flower bud formation. On the contrary it is obvious that red light is even more active than blue light, ½ hour of red light (10B 7½D ½r) being already sufficient where 2 hours of blue light (10B 6D 2b) were ineffective. The ineffectiveness of 8 hours of supplemental red light (10B 8r) in producing a long-day effect might be caused by:

a) the absence of a dark period between the main light period and the supplemental light period, or
b) an antagonizing effect of red light (the first four hours of —8r).

In the following experiment plants were exposed to a short-day treatment of 8 hours of blue light per day (8B) with an intensity of 580 μW/cm^2. In the 8-hour period after this main light period the plants were

a) kept in darkness (8B) or treated with
b) 4 hours of darkness followed by 4 hours of red light (8B 4D 4r),
c) 8 hours of red light (8B 4r 4r)
d) 4 hours of blue followed by 4 hours of red light (8B 4b 4r),
e) 8 hours of blue light (8B 4b 4b) or
f) 4 hours of blue light followed by darkness (8B 4b 4D).

The intensity of both the blue and the red additional light was 200 μW/cm^2. After this 8-hour period all plants were kept in darkness for the remaining 8 hours per day. The treatment lasted 29 days after which the plants were transferred to long days. The last observations were made after 59 days.

The results presented in Table 14 (Plate 2 f) showed that the long-day effect of the last 4 hours of red light (8B 4D 4r) is prevented if it is preceded by 4 hours of red light (8B 4r 4r). 4 Hours of blue light given immediately after the main light period (8B 4b 4D) —which in itself did not cause any long-day effect—did not influence the activity of a following exposure to 4 hours of red light (8B 4b 4r).

TABLE 14

Photoperiodic effect of blue and red light (200 μW/cm^2) given in an 8-hour period after a main light period of 8 hrs blue light (580 μW/cm^2). Duration of the treatment 29 days. Number of plants per treatment 3. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 59 days.

Light treatment in hrs per day			Condition of the growing point		
Main light period 8 hrs per day	Supplemental 8-hour period				
8B	4D	4D	+	+	+
8B	4D	4r	—	—	—
8B	4r	4r	+	+	+
8B	4b	4r	—	—	—
8B	4b	4b	—	—	—
8B	4b	4D	+	+	+

Obviously, red light is more active than blue light in causing a long-day effect provided it is not given immediately after the main light period.

3.1.3 NIGHTBREAK TREATMENT

The influence of the light quality of the main light period on the photoperiodic effect of a nightbreak treatment was studied in the following experiments with *Salvia occidentalis*. Red light was used to interrupt the long dark period as it had been shown to be the most active in causing a long-day effect.

Six lots of plants were exposed to short days of 8 hours of red, green or blue light per day with and without a simultaneous addition of near infra-red radiation. Some of the plants of each group were irradiated with 15 minutes red light to interrupt the corresponding long dark period from 7.45 hours–8 hours after its beginning. The intensity of the light of the main light period was 450 μW/cm^2, of the near infra-red 200 μW/cm^2 and of the red nightbreak light 630 μW/cm^2. The number of plants per treatment was 3. After the experiment had lasted 25 days, the plants were transferred to long days. After 50 days the last observations were collected. The results are presented in Table 15. (Plate 2–g). The generative plants formed

TABLE 15

The influence of the light quality of an 8-hour main light period on the photoperiodic effect of a night interruption with 15 minutes red light (15′R). Intensity of the visible radiation of the main light period 450 μW/cm^2 and of the near infra-red 200 μW/cm^2. Intensity of the red nightbreak light 630 μW/cm^2. Duration of the treatment: 25 days. 3 Plants per treatment. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 50 days.

Main light period in hrs per day	Nightbreak light					
	dark control			15′R		
8R	+	+	+	+	+	+
8RIR	+	+	+	+	—	—
8G	+	+	+	+	+	+
8GIR	+	+	+	—	—	—
8B	+	+	+	—	—	—
8BIR	+	+	+	—	—	—

about 5 leaf pairs before flowering was initiated, the vegetative plants had developed 9 or 10 new pairs of leaves after 50 days.

It is clear that an interruption of the long dark period with red light (—15′R) is only effective in preventing flowering when the preceding main light period contained blue or near infra-red radiation (8B–15′R or 8GIR–15′R).

In experiments with white fluorescent light it was often noted that under certain conditions this light is less active in causing a long-day effect than, e.g. natural day-light.

In the next experiments the plants were kept in short days of
a) 10 hours of blue light (10B) with an intensity of 670 μW/cm², or
b) 10 hours of white fluorescent light (10W) with an intensity of 3250 μW/cm².

From both groups some plants were kept in darkness for the remaining 14 hours (10B, 10W). Other plants of each group were irradiated with red nightbreak light. This light was given only from above; the intensity was 185 μW/cm². This irradiation lasted thirty minutes (—30′R), 60 minutes (—60′R) or one hundred and twenty minutes (—120′R) and was given from respectively 7½, 7 and 6 hours up to 8 hours after the beginning of the long night period of 14 hours. The treatment was finished after 26 days; the last observations were made after 80 days. The results are given in Table 16. The generative plants developed 5 to 7 pairs of leaves before flower buds appeared; the plants which remained vegetative showed 13 or 14 newly formed leaf pairs at the end.

TABLE 16

Photoperiodic effect of red nightbreak light (185 μW/cm²) as influenced by the preceding short-day period of 10 hrs blue (670 μW/cm²) or 10 hrs white fluorescent light (3250 μW/cm²) per day. Duration of the treatment: 26 days. 3 Plants per treatment. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 80 days.

Main light period in hrs per day	Nightbreak light (minutes per night)			
	dark	30′R	60′R	120′R
10B	+ + +	— — —	— — —	— — —
10W	+ + +	— + +	+ + —	+ — —

The plants exposed to short days in blue light, proved that a night interruption with 30 minutes of weak red light (10B–30′R) was enough to cause a long-day effect. If, however, the plants were grown in 10 hours of white light per day, it was found that even a night interruption with 120 minutes of red light (10W–120′R) was not completely effective in preventing flowering; only two plants remained vegetative.

It may be noted here that the intensity of the white light was about five times the blue light intensity. As calculated from the emission spectrum of the lamp ("TL" 80W/33), white fluorescent light contains 25 % blue radiation in the wave-length region of $\lambda = 4000$–5000 Å i.e. about 800 μW/cm². This was even higher than the intensity of 10B (670 μW/cm^2) for which a nightbreak with 30 minutes of weak red light was sufficient to cause a long-day effect.

As was shown in experiments mentioned before, both blue and near infra-red radiation are active in the same way: the activity of both can be antagonized by red light. The following experiments were carried out to determine whether the long-day effect of a night interruption with red light can be counteracted by a following exposure to blue in a similar way as by an exposure to near infra-red, the antagonistic effect of the latter having been proved for many plant species.

The plants were grown in 10 hours of blue light per day (10B). Five hours after the beginning of the long dark period groups of 4 plants were exposed to 10 minutes of red nightbreak light (–10′R) after which 0 minutes (10B–10′R), 15 minutes (10B–10′R15′RI) or 30 minutes (10B–10′R30′IR) near infra-red radiation were given. Other groups were not exposed to the red nightbreak light but only to 15 or 30 minutes near infra-red radiation (10B–15′IR and 10B–30′IR). In another experiment the plants were treated with 15, 30 or 60 minutes of blue light instead of near infra-red radiation. (10B–10′R15′B; 10B–15′B etc.). The intensity of the blue light was 580 μW/cm^2, of the red light 700 μW/cm^2 and of the near infra-red, obtained from a neon lamp, 175 μW/cm^2. The treatment lasted 25 days after which the plants were returned to long-day conditions; the last observations were made after 56 days.

The results of the experiment with near infra-red are given in Table 17 (Plate 2–h). The generative plants developed 4 or 5 pairs of leaves before flower buds appeared. After 56 days the vegetative plants showed 10 newly formed pairs of leaves.

TABLE 17

The antagonizing activity of near infra-red (175 μW/cm^2) on the long-day effect of a nightbreak with 10 minutes red light (700 μW/cm^2) after a main light period of 10 hrs blue light (580 μW/cm^2). Duration of the treatment 25 days. Number of plants per treatment 4. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 56 days.

Main light period in hrs per day	Night interruption in minutes per night		Condition of the growing point			
10B	—	—	+	+	+	+
10B	10′R	—	—	—	—	—
10B	—	15′IR	+	+	+	+
10B	10′R	15′IR	+	+	+	+
10B	—	30′IR	+	+	+	+
10B	10′R	30′IR	+	+	+	+

It is obvious that in *Salvia occidentalis*, too, the long-day effect of a night interruption with red light (10B–10′R) is nullified by a following exposure to near infra-red (10B–10′R15′IR) and 10B–10′R30′IR). The near infra-red radiation itself (10B–15′IR and 10B–30′IR) did not show a photoperiodic effect under these conditions as flower initiation was not prevented.

As can be seen in Table 18 (Plate 2–h) blue light too was effective in antagonizing the effect of red nightbreak light. In this experiment the generative, respectively vegetative, plants developed about the same number of leaves as the corresponding plants in the foregoing experiment.

TABLE 18

The antagonizing activity of blue light (580 μW/cm^2) on the long-day effect of a night interruption with 10 minutes red light (700 μW/cm^2) after a main light period of 10 hrs blue light (580 μW/cm^2). Duration of the treatment: 25 days. 4 Plants per treatment. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 56 days.

Main light period in hrs per day	Night interruption in minutes per night		Condition of the growing point			
10B	—	—	+	+	+	+
10B	10′R	—	—	—	—	—
10B	—	15′B	+	+	+	+
10B	10′R	15′B	+	—	[illegible]	—
10B	—	30′B	+	+	+	+
10B	10′R	30′B	+	+	+	+
10B	—	60′B	+	+	+	+
10B	10′R	60′B	—	—	—	—

A nightbreak with blue light did not cause a long-day effect (10B–15′B . . . 10B–60′B). However, 30 minutes of blue light were sufficient to antagonize the long-day effect of a foregoing exposure to 10 minutes of red light (10B–10′R30′B). It is remarkable that a longer exposure to blue light, viz. 60 minutes did not nullify this long-day effect of 10 minutes of red nightbreak light (10B–10′R60′B).

In the following experiments the photoperiodic effect of near infra-red, given as nightbreak light, is demonstrated. Two groups of plants were daily exposed to 8 hours of red light (8R) or to 8 hours of red light, followed immediately by one hour of near infra-red (8R1IR). Seven hours and 20 minutes after the end of the main light period lots of 4 plants, treated daily with 8R1IR, were exposed to

a) 10 minutes of red nightbreak light (8R1IR–10′R),
b) 10 minutes of red followed by 15 minutes of near infra-red (8R1IR–10′R15′IR) or followed by
c) 60 minutes of near infra-red (8R1IR–10′R60′IR) and
d) 60 minutes of near infra-red without preceding red light (8R1IR–60′IR).

The intensity of the red radiation during the main light period was 670 μW/cm^2, of the red nightbreak light 700 μW/cm^2 and of the near infra-red radiation, obtained from neon lamps, 200 μW/cm^2. The treatment lasted 25 days, the last observations were made after 55 days. The results are presented in Table 19A (Plate 2–i).

Separate lots of 4 plants, treated with a short daily light period of 8R, were

a) kept in darkness during the remaining 16 hours per day (8R) or exposed to

b) 10 minutes of red light (8R–10′R) and
c) 10 minutes of red followed by 60 minutes of near infra-red (8R–10′R60′IR), both treatments started 20 minutes past the middle of the dark period;
d) 30 minutes of red (8R–30′R) and
e) 30 minutes of red followed by 60 minutes of near infra-red (8R–30′R60′IR), both treatments started at the middle of the night period;
f) 60 minutes of red (8R–60′R) and
g) 60 minutes of red followed by 60 minutes of near infra-red (8R–60′R60′IR), both treatments started 30 minutes before the middle of the night period;
h) 60 minutes of near infra-red (8R–60′IR) given at the same time as in *c*, *e* and *g*, i.e. 8½ hours after the beginning of the long dark period.

TABLE 19 A AND B

The influence of a nightbreak with red (700 μW/cm²) and/or with near infra-red (200 μW/cm²) after a main light period of A: 8 hrs red light (670 μW/cm²) + 1 hr near infra-red (200 μW/cm²) or B: 8 hrs red light (670 μW/cm²). Duration of the treatment: 25 days. 4 Plants per treatment. + = generative (short-day effect); — = vegetative (long-day effect). Observations after 55 days.

Main light period in hrs per day	Night interruption in minutes per night		Condition of the growing point			
A						
8R 1IR	—	—	+	+	+	+
8R 1IR	10′R	—	—	—	—	—
8R 1IR	10′R	15′IR	+	+	+	+
8R 1IR	—	60′IR	—	—	—	—
8R 1IR	10′R	60′IR	—	—	—	—
B						
8R	—	—	+	+	+	+
8R	—	60′IR	+	+	+	+
8R	10′R	—	+	+	+	+
8R	10′R	60′IR	+	+	+	+
8R	30′R	—	+	+	+	+
8R	30′R	60′IR	+	+	+	—
8R	60′R	—	+	+	+	+
8R	60′R	60′IR	—	—	—	—

The conditions were just the same as described above; the results of this experiment are given in Table 19B (Plate 2–i). In both experiments the generative plants developed 5 or 6 new pairs of leaves before flower buds were initiated; the plants which remained vegetative showed, 55 days after the beginning of the treatment, about 9 or 10 newly formed leaf pairs.

As can be seen in Table 19, a night interruption with –10′R was only effective in causing a long-day effect when given in co-operation with a main light period of 8R1IR (8R1IR–10′R) but not with 8R (8R–10′R). With 8R, a nightbreak with even 60′R was not effective, flowering being not prevented.

Moreover it was found that a nightbreak with –60′IR was photoperiodically active when given in combination with a main light period of 8R1IR as a long-day effect was obtained (8R1IR–60′IR). In co-operation with a main light period of 8R, a night interruption with 60′IR was not effective in this respect (8R–60′IR). If, however, the –60′IR was preceded by –60′R a long-day effect was obtained (8R–60′R60′IR), in spite of the ineffectiveness of each component (–60′R and –60′IR) when used separately. 60′IR after –30′R caused some prevention of flowering (8R–30′R60′IR).

Obviously the effect of red nightbreak light can be counteracted by a subsequent exposure to near infra-red or blue light. It was also shown that under certain conditions near infra-red radiation can be active as nightbreak light.

3.1.4 EXPERIMENTS WITH OTHER PLANTS

Some experiments were carried out with other plants than *Salvia occidentalis*.

Long-day experiments with *Hyoscyamus niger* (LDP) confirmed the results of STOLWIJK *et al.* (1955) and CURREY *et al.* (1956), blue or near infra-red radiation being necessary for obtaining a long-day effect. In nightbreak experiments it was shown that red nightbreak light was only effective in causing a long-day effect when it was given in combination with a main light period in blue light (10B–10′R), the effect of near infra-red was not investigated (MEIJER *et al.* 1957). In experiments with supplemental light, the plants were daily exposed to a short day (main light period) in red, green, blue (490 μW/cm^2) or green + near infra-red (160 μW/cm^2) after which the plants were kept in darkness or exposed to 8 hours of red or blue light (165 μW/cm^2). It was found that blue supplemental light did not cause a long-day effect and that red supplemental light was only effective in this respect when it was preceded by either 10 hours blue (10B 8r) or 10 hours of green + near infra-red (10GIR 8r).

Petunia hybr., a non-obligate long-day plant, exposed to long days (16 hours light per day) in red, green, blue or green + near infra-red (400 μW/cm^2), started bolting almost immediately in 16B or 16GIR and flowering was obtained about 6 weeks after the beginning of the treatment. In 16R or 16G the plants remained in the rosette form; no flowering occurred, even not after 4 months when the treatment was discontinued. The elongation in 16B and 16GIR is not a long-day effect because it also results from a short-day treatment (10 hours of light per day). In this case, however, no flowering was obtained.

With *Chrysanthemum parthenium* (LDP) it was found that a long-day treatment in red, green or blue light (700 μW/cm^2) resulted in a long-day effect. In blue light, however, flowering was accelerated as in 16B flower buds were visible after 19 days, in 16R and 16G after 29 days.

Similar results were obtained with representatives of the *Crucifereae*.

In long-day experiments with *Sinapis alba* (LDP), with a light intensity of 610 μW/cm^2 it was found that blue light accelerated flowering when compared with red or green light: in 16B plants showed flower buds after 15 days, in 16R or 16G after 32 days. With a light intensity of 250 μW/cm^2, in 16B the flower buds were visible after 27 days, whereas in 16R or 16G the plants remained vegetative even after two months.

A long-day treatment of *Nasturtium palustre* (LDP) with red, green, blue or green + near infra-red at an intensity of 450 μW/cm^2 showed that a long-day effect was only obtained when the plants were exposed to blue or near infra-red radiation. At an intensity of 700 μW/cm^2, however, 16R was also effective in causing a long-day effect.

Of *Arabidopsis thaliana* (LDP) three strains of different origin were compared. At an intensity of 470 μW/cm^2 only one strain initiated flower buds in 16B and in 16BIR. In the other two varieties flowering was only obtained when near infra-red was given simultaneously with the blue light (16BIR). One of these less sensitive strains initiated flowering in 16B when the intensity was raised to 650 μW/cm^2. In 16R or 16G (470 or 650 μW/cm^2) all three varieties remained vegetative.

Some other plant species as *Kalanchoë blossfeldiana*, *Euphorbia pulcherrima* and *Xanthium pennsylvanicum*, all short-day plants, did not show this spectral dependence under our experimental conditions.

Obviously the requirement of blue or near infra-red for obtaining a long-day effect is not restricted to *Salvia occidentalis* and *Hyoscyamus niger*, although there seem to exist plants which do not show this spectral dependence.

3.1.5 DISCUSSION

1. *Dual effect of light on flower formation*

Several authors have observed that the flower formation of various plants does not depend on light but even occurs in darkness (BORGSTRÖM 1939; LANG *et al.* 1943; LEOPOLD 1949, 1952; FIFE *et al.* 1953).

TASHIMA (1953, — *et al.* 1953) sowed and cultivated *Pharbites Nil* (SDP) and *Raphanus sativus* (LDP) on a culture medium in complete darkness. Under these conditions flower initiation occurred. When the plants were irradiated, however, no flowering was initiated unless the plants were exposed to an inducing daylength, i.e. *Pharbites* to short days, *Raphanus* to long days. No differences were observed between the plants in darkness and those in the inducing daylength as far as the flower initiation was concerned. Similar results were obtained with some other long-day plants. Apparently light inhibits flower formation, which inhibiting effect can be antagonized by a certain light treatment (photoperiodic reactions).

2. *Light intensity and photoperiodic response*

Whether a light treatment is succesful or not in inducing flower formation does not depend on the daylength only (photoperiodic reactions), but also on the light intensity (photosynthesis).

In the case of *Xanthium pennsylvanicum* (SDP), HAMNER (1940) demonstrated that flower formation was only obtained after an inductive long dark period (short-day treatment) if this had been preceded by a light period of a sufficiently high light intensity. This light of high-intensity could be replaced by a supply of carbohydrates. Therefore it was concluded that in this case the photoperiod is only necessary to produce sufficient photosynthates. (BONNER *et al.* 1953). Hence the absence of flower formation in our experiments with *Salvia occidentalis*, exposed to a light intensity of 85 μW/cm^2 (Tables 3 and 4), may also be due to a lack of photosynthates.

In experiments with *Perilla* (DE ZEEUW, 1953) and *Salvia* (Table 2), both short-day plants, it was found that with a long-day treatment no long-day effect was obtained when the light intensity was too low. From the experiments described in this paper it is obvious that this phenomenon is not caused by the decrease of photosynthesis (Table 3).

3. *Short-day treatment*

Information on the spectral dependence of the effect of a short-day treatment is scanty. WALLRABE (1944), using *Kalanchoe* (SDP) has reported that blue light was more active than red light in causing a short-day effect, green light being not active in this respect. She supposed some relation to exist between the photoperiodic response and photosynthesis. Short-day experiments with *Salvia occidentalis* (SDP) and *Kalanchoe* did not confirm this spectral dependence of the short-day effect (MEIJER *et al.* 1957). It is possible, however, that during these experiments the light intensity was too high for obtaining a possible dependence of the photoperiodic response on wave length.

4. *Long-day treatment*

The spectral dependence of the activity of a long-day treatment which has been demonstrated by STOLWIJK *et al.* (1955) and CURREY *et al.* (1956) in the case of *Hyoscyamus niger* (LDP) was confirmed for *Salvia occidentalis* (SDP) and some long-day plants. Long-day experiments with *Salvia* in coloured light at different intensities (Table 3) show that:

1°. all spectral regions are active in producing a long-day effect;
2°. near infra-red and blue light are, however, the most active types of light in this respect. Red light is less effective whereas green light is only slightly active (Plate 1–a).

Similar results were obtained with the long-day plants *Arabidopsis thaliana*, *Nasturtium palustre* and *Sinapis alba* (3.1.4).

In the case of *Kalanchoe* and *Euphorbia* (both SDP) a long-day treatment was equally effective in red, green or blue light. Judging from the response of the other plant species used it is possible that the light intensity to which these two species were exposed was too high, to find a spectral dependence.

5. *Nightbreak treatment*

It has been shown that red light is more active than blue light when it is used to interrupt the long dark period after a short day in white light (e.g. PARKER *et al.* 1950). This spectral dependence of nightbreak light was confirmed for both *Hyoscyamus* (STOLWIJK *et al.* 1955) and *Salvia* (MEIJER 1957*a*).

STOLWIJK *et al.* supposed that for obtaining a long-day effect not only the blue, near infra-red reaction was required because a short-day treatment in light of these wave-length regions did not result in causing a long-day effect. They suggested that "an additional photoperiodic stimulus is required . . .".

In the present paper it is clearly demonstrated that for obtaining a long-day effect at least two photoreactions with a different spectral sensitivity are required. In nightbreak experiments with *Salvia* and *Hyoscyamus* it was observed that red nightbreak light was only effective in combination with a main light period (short day) in blue or in green + near infra-red. After a main light period in red or in green light, a night interruption with red light did not cause a long-day effect (Plate 2–g).

Hence it may be concluded that it depends on at least two photoreactions whether a long-day effect will be obtained or not, viz.:

1° a "main-light-period reaction" which is most sensitive to near infra-red and blue radiation;

2° a "nightbreak reaction", in which red light is the most promotive spectral region.

In the case of a long-day treatment with e.g. 16B it seems as if the "main-light-period reaction" is already sufficient to cause a long-day effect. Although red light is the most active wave-length region in inducing the "nightbreak reaction", the other spectral regions too are active, even near infra-red (CATHEY *et al.* 1958), but to a much lesser extent. For this reason both reactions can occur when the plants are exposed to 16B. The first 10 hours of blue light will induce the main-light-period reaction, whereas the last part of the 16-hour photoperiod will be sufficient, even in blue light, to cause the nightbreak reaction.

The long-day effect of 16R and 16G (provided that the light intensity is sufficiently high) can be explained in a similar way: the last 6 hours of red "nightbreak" light may be sufficient for obtaining a long-day effect after a weak main-light-period reaction caused by the first 10 hours of red light.

6. *Relation between the two reactions*

The quantitative relation between both reactions assumed above is confirmed by the observation that the effect of a certain amount of nightbreak light depends on the intensity of the main-light-period reaction. It was found that 30 minutes of nightbreak light of low intensity was sufficient after a main light period of 10 hours of blue light but insufficient after a main light period of 10 hours of white light. (Table 16). A main-light-period reaction, however, was also induced by white light but for obtaining a long-day effect more nightbreak light was necessary. The data presented in Table 11 and 12 confirm this conclusion. Besides, these data demonstrate that near infra-red is more active than blue light in inducing the main-light-period reaction, a main light period of 8GIR being more effective than a main light period of 8B.

In addition to the dependence of the nightbreak reaction on the intensity of the main-light-period reaction, yet another correlation between both reactions was observed. It has been reported that nightbreak light is the most active when used near the middle of the long dark period. The closer the moment of nightbreak to the beginning or the end of the dark period, the higher the light intensity necessary for obtaining a long-day effect (e.g. Könitz, 1958). This influence of the time interval is clearly demonstrated in the experiment presented in Table 7 (see also Plate 1–b). One hour near infra-red given alternately with green light only causes a long-day effect if:

1° the near infra-red period is preceded by some hours of light (Plate 1–b, region between dotted lines); the influence of this light period is unknown, but it may be necessary for the production of carbohydrates and

2° light is given in a period, 8 to 10 hours after the beginning of the near infra-red period (region between broken lines).

In preliminary experiments *Salvia* was exposed to a main light period of 8G 1IR. It was observed that 10 minutes of red light was not effective in causing a long-day effect when given 7½ hours after the beginning of the near infra-red irradiation. When used one hour later, however, it was effective in this respect. The dependence of the long-day effect on both conditions mentioned above is also demonstrated in experiments presented in Plate 2–i.

It is supposed that near infra-red or blue light induces the main-light-period reaction, the green or red light being active in causing a nightbreak reaction but only when given a certain number of hours after the main-light-period reaction was induced.

7. *Supplemental light treatment*

A supplemental light treatment with low light intensity may be conceived as a nightbreak treatment, the dark period between the main light period and the nightbreak being filled up with light. This conception is supported by the spectral dependence. It has been reported for almost all plant species that red light is more active in producing a long-day effect than blue light, either as a night interruption or as supplemental light.

An exception, however, has been reported for a number of plants, all belonging to the Cruciferae (Funke, 1948). For these plants it was noted that on the contrary blue supplemental light is photoperiodically more active than red supplemental light. Wassink *et al.* (1950) and Stolwijk (1954) confirmed this activity of blue light, used as supplemental light, for some other cruciferous plants and observed an activity of near infra-red radiation too, in this respect.

In this paper results obtained from long-day experiments with three *Cruciferae* (3.1.4) show the same blue and near infra-red sensitivity. It may well be that representatives of this plant family are exceptional in their response to light in that only the "main-light-period reaction" is involved in the process leading to a long-day effect. However, as far as known, no nightbreak experiments with Cruciferae have been carried out in coloured light. Experiments with *Hyoscyamus* showed that this exceptional spectral dependence of supplemental light is not restricted to the Cruciferae, near infra-red being more active in causing a long-day effect than red light (Stolwijk *et al.* 1955).

For *Salvia occidentalis* the same spectral dependence was observed as found for the *Cruciferae*, blue light being more active in causing a long-day effect than red light (Plate 1–d). In the nightbreak experiments it was found that red light was more active than blue light (Plate 2–g). However, as far as *Salvia occidentalis* is concerned it was demonstrated that the exceptional spectral dependence was only apparent. Experiments in which the supplemental light period was shortened and a dark period was inserted between the main light period and the "supplemental light" demonstrate that the inactivity of a treatment with red supplemental light was not caused by any inactivity of the red light, but was due to an antagonizing effect of the red light on the main-light-period reaction induced by blue light (Plate 2–e, f).

Hence it is obvious that the photoreaction activated by supplemental light is just the same as the photoreaction activated by a nightbreak. It is quite probable that the results of Funke, of Wassink *et al.* and those of Stolwijk mentioned above are also due to the antagonizing effect of red light on the main-light-period reaction.

8. *Antagonism*

a. Main-light-period reaction

This antagonizing activity of red light on blue light is also demonstrated in long-day experiments (Plate 1–c). Blue light, given supplementarily after green light (15G 1B), caused a long-day effect. This activity of blue light was reversed by subsequent exposure to red light (15G 1B 1R). In similar experiments the antagonizing activity of red light on the effect induced by near infra-red was shown (Plate 1–c). 15G 1IR caused a long-day effect which was nullified by a subsequent exposure to red light (15G 1IR ½R).

The lower activity of white light, as compared to blue light, in causing a long-day effect (Table 16), may be due to the antagonizing effect of red on blue light. Wassink *et al.* (1957) too, have demonstrated this antagonizing activity in long-day experiments with *Hyoscyamus*. Red light, given simultaneously with blue light prevented the long-day effect caused by blue light.

b. Nightbreak reaction

An antagonism comparable to that described above for the main-light-period reaction has already been shown for the nightbreak reaction, near infra-red antagonizing the effect of red nightbreak light (Borthwick *et al.* 1952). This antagonizing activity of near infra-red, demonstrated with various plants, is confirmed in the case of *Salvia occidentalis* (Plate 2–h) and *Hyoscyamus niger* (STOLWIJK *et al.* 1955).

In experiments described in this paper it was observed that blue light too can nullify the effect of red nightbreak light (Plate 2–h). This antagonizing effect of both blue and near infra-red is in agreement with the results obtained from experiments on the germination of seeds (FLINT *et al.* 1935, WAREING *et al.* 1958) and of fern spores (MOHR 1956).

9. *Dual role of light*

It appears, however, that blue light does not only antagonize the nightbreak reaction induced by a preceding night interruption with red light. It has been demonstrated that light of this wave-length region is also effective in promoting the nightbreak reaction, a much larger amount of energy being necessary than with red light (PARKER *et al.* 1950). This promotive activity of blue light is also shown in this paper (Plate 2–e).

A similar antagonizing activity (BORTHWICK *et al.* 1952) and promoting activity (CATHEY *et al.* 1957) of near infra-red radiation used as nightbreak light was reported and confirmed for *Salvia occidentalis*. In Table 19A (Plate 2–i) both the antagonizing and the promotive activity of near infra-red on the nightbreak reaction are demonstrated.

Concerning the main light period it is obvious that red light not only counteracts the promoting effect of blue or near infra-red (Plate 1–c), but can also induce the main-light-period reaction, although to a much lesser extent than blue or near infra-red. A long-day effect with 16 hours red light per day is only obtained with relatively high light intensities (Table 3).

So it will depend on the amount of light whether an antagonizing or promoting effect is obtained: of blue and near infra-red on the nightbreak reaction and of red light on the main-light-period reaction.

10. *Conditions for obtaining a long-day effect*

From the data discussed above it may be concluded that for obtaining a long-day effect the following conditions must be fulfilled:

a. a main-light-period reaction must be present (Table 20);
b. a nightbreak reaction must take place (Table 20);

TABLE 20

The spectral dependence of the two photoreactions required for obtaining a long-day effect.

1. Main-light-period reaction		2. Nightbreak reaction	
Promoted by	Promotion nullified by	Promoted by	Promotion nullified by
Near infra-red, Blue (Red *)	Red	Red (near infra-red,* Blue *)	Near infra-red, Blue

* Slightly active.

c. a certain number of hours must elapse between the main-light-period reaction and the nightbreak reaction (Plate 1–b, see also page 219).

Besides, it was noted that the amount of nightbreak light necessary for obtaining a long-day effect depends on:

1° the number of hours between the main light period and the night interruption (e.g. Könitz 1958) and

2° the intensity of the main-light-period reaction (Table 16).

11. *Critical daylength*

During experiments with *Chenopodium amaranticolor* (SDP), it was found that flower initiation occurred when the plants were exposed to 13 hours of "white" light per day (Könitz 1958). This light was obtained from fluorescent lamps. Its emission spectrum shows that about the same amount of energy is emitted in the blue and in the red part of the visible spectrum. It may be noted here that the relative amount of near infra-red radiation present in this white light is very much less than in natural daylight or in "white" light obtained from incandescent lamps.

In this daylength, however, flower initiation was prevented when the 13-hour light period was interrupted with near infra-red radiation. Thus a long-day effect was obtained. Moreover it was shown that near infra-red was the most active spectral region when given around the fifth hour after the beginning of the light period and that red light nullified this effect of near infra-red radiation.

This experiment shows a typical resemblance with the experiment in which *Salvia* was exposed to 16G (flower initiation occurring i.e. no long-day effect) and 6G 1IR 9G (flower initiation prevented, i.e. long-day effect, Plate 1–b). It is obvious that in Könitz's experiment the inactivity of 13 hours of white light per day in producing a long-day effect was caused by the "absence" of near infra-red.

It is supposed that in fluorescent light both photoreactions were not sufficiently intensive because of

1° the lack of near infra-red and

2° the antagonizing activity of light of one spectral region on the effect of light of another spectral region.

Therefore no long-day effect could be obtained. After the near infra-red had been supplied the main-light-period reaction may have been induced, the last hours of the photoperiod acting as a nightbreak and in this way a long-day effect was obtained. This assumption is also supported by the observations of Roodenburg (1954), Takimoto (1957) and Wassink *et al.* (1951) and Table 16 of this paper. Takimoto found that *Silene armeria* (LDP) did not initiate flower buds in a long-day treatment of 18 hours per day in "white" fluorescent light. With the same daylength a long-day effect was obtained when part of the irradiation with fluorescent light was replaced by incandescent light. As already mentioned, incandescent lamps emit relatively much larger amounts of near infra-red than fluorescent lamps. In the experiments of Wassink *et al.* with *Brassica* it was demonstrated that a short-day treatment in white fluorescent light did not cause a long-day effect. If, however, part of the white fluorescent light was replaced by blue + near infra-red, a long-day effect was obtained.

The experiments of WASSINK *et al.* and KÖNITZ mentioned above demonstrate that even a short-day treatment can cause a long-day effect, depending on the light quality of the photoperiod. The relative value of the "critical daylength" was also shown in the experiments of TAKIMOTO (1957) and in our experiments which show that the light quality largely determines whether a long-day effect is obtained or not.

Evidently the long-day effect does not simply depend on the length of the photoperiod or that of the dark period, but on the conditions mentioned in 10.

12. "*Endogenous Diurnal Rhythm*"

As far as the long-day effect is concerned it is obvious that during a certain part of a natural 24-hour cycle the plant will be in a condition in which blue and near infra-red are promoting and red light is inhibiting the process leading to the long-day effect. In a following period the plant is in a condition in which, on the contrary, red light has a promotive effect and blue and near infra-red may inhibit this promotive effect. Both periods with different spectral sensitivities (Table 20) alternate with each other in a 24 hour rhythm. The results in Table 19 (Plate 2–i) show that the alternating periods may even be interchanged: the "main-light-period reaction" is not only induced by the main light period but, under certain conditions, also by the original nightbreak light period. The original main light period will be active in inducing the nightbreak reaction (region between broken lines). 8R 1IR will cause the main-light-period reaction and 10′R or 60′IR the nightbreak reaction. It is obvious, however, that the original main light period is not effective when the near infra-red is omitted (8R), as under this condition 10′R or 60′IR are not active in causing a long-day effect. If, however, the 60′IR of nightbreak light are preceded by 60′R, it is probable that this combination will induce the main-light-period reaction and the original "main light period" will induce the nightbreak reaction. This assumption is supported by the requirement of supplying a certain amount of light prior to the near infra-red, which was already shown on page 219. In this case 10′R are insufficient, whereas 60′R appear to be sufficient, 8R–10′R60′IR not causing, 8R–60′R60′IR causing a long-day effect.

These alternating periods with a different spectral sensitivity show a 24-hour rhythm. The phase of the rhythm appears to be controlled by radiation. This is in agreement with the theory of the "Endogenous Diurnal Rhythm" developed by BÜNNING (1958).

13. *Photoreactions and Pigments*

From the two photoreactions mentioned above, the one which is involved in the nightbreak reaction is governed by the red-absorbing pigment controlling so many phenomena (see 1.1). According to BORTHWICK *et al.* (1954), the effect of an irradiation with red light is antagonized as soon as near infra-red is supplied and this antagonism appeared to be reversible. For this reason these authors suggested that only one pigment be involved, which would be converted into a near infra-red absorbing form (P′) after having absorbed red light. The near infra-red absorbing form would be converted into the red absorbing form (P) after irradiation with near infra-red.

From the data presented in this paper it is obvious that the red absorbing form (P) of the pigment is not only regenerated by irradiation with near infra-red but also with blue light:

$$P \underset{\text{IR, B}}{\overset{\text{R}}{\rightleftarrows}} P'$$

The main-light-period reaction will be governed by a pigment absorbing blue and near infra-red. The antagonizing effect of red light on the effect of blue and near infra-red might also be caused by a pigment conversion, similar to that suggested for the nightbreak reaction.

No decisive answer can be given to the question whether two different pigment systems are involved, one in the main-light-period reaction, the other in the nightbreak reaction, or two different forms of one pigment. In the latter case a long-day effect can only be explained by assuming that both forms of the pigment alternately replace each other in a 24-hour rhythm. The reported data do not indicate, which of either possibility has the best chance of being correct, nor do they yield any indications about the character of the pigment(s).

3.2 Elongation

3.2.1 Introduction

In the beginning of the study of the influence of light quality on elongation, various plant species, plants previously raised in white light, have been used. The plants were exposed to 16 hours per day of red, green or blue light with and without a simultaneous addition of near infra-red radiation. After the treatment had lasted for some time the length of the internodes was measured. The results obtained from experiments with several plant species are given in Table 21. The intensity of the visible radiation was 475 $\mu W/cm^2$ and of the near infra-red 120 $\mu W/cm^2$.

It was found that the effect of light of different spectral regions varied with the plant species. In the case of gherkin and *Salvia occidentalis* elongation was much less inhibited in blue light than in red or green light. Near infra-red stimulated elongation, especially when it was added to green (gherkin) or to green or blue light (*Salvia*). Other plant species which reacted in a similar way are *Petunia, Calendula*, *Perilla*, *Helianthus* and bean.

Mirabilis jalapa on the other hand showed a marked elongation in red and in green light, while in blue light the internodes were much shorter. Near infra-red was slightly active in promoting the elongation only when it was added to blue light. *Rivina humilis* and *Mentha longifolia* reacted in a similar way.

TABLE 21

The influence of an irradiation (16 hours per day) with red (16R), green (16G) and blue light (16B), with or without near infra-red (IR), on the elongation of light-grown plants. Intensity of visible radiation 475 $\mu W/cm^2$ and of near infra-red 120 $\mu W/cm^2$. Length in mm, N days after the beginning of the treatment (second column).

Plant species	N	Light treatment in hrs per day					
		16R	16RIR	16G	16GIR	16B	16BIR
Gherkin (hypocotyl) 5 days *	8 days	23	36	26	101	79	81
Mirabilis jalapa (1st internode) 14 days *	30 days	182	179	174	188	128	153
Salvia occidentalis (internode) 20 days *	30 days	42	60	43	82	64	90
Tomato (hypocotyl) 14 days *	11 days	27	29	24	54	28	42
Tomato (1st internode) 14 days *	15 days	69	74	62	63	38	38

* Age of the plants at the beginning of the treatment.

The hypocotyls of tomato plants reached about the same length in red, green or blue light. The assumption that this hypocotyl was already fully developed cannot be valid, an addition of near infra-red to green or blue light causing an increase in length. The first internodes of the same tomato plants, however, reacted in about the same way as in the case of *Mirabilis;* near infra-red given simultaneously did not have any effect. At the beginning of the treatment with coloured light this first internode was in a younger stage of development than the hypocotyl. For this reason it was possibly less affected by the pretreatment with white light than the hypocotyl.

Experiments with gherkin seedlings demonstrated that, after sowing in coloured light, the difference in length between plants grown in red and plants grown in blue light was much smaller than after sowing in white light. The higher the light intensity the smaller the difference in length.

Bean plants sown in coloured light became somewhat longer in red than in blue light; with light-grown bean plants, however, the reversal result was obtained: the internodes were longer in blue than in red light.

So the question arose whether a pretreatment with white light influences the effect of a subsequent exposure to light of different spectral regions and whether this effect depends on the intensity of the coloured light.

3.2.2 DIFFERENT LIGHT INTENSITIES

In the following experiments various plant species, either previously raised in white light ("light-grown plants") or immediately sown in coloured light ("dark-grown plants") were exposed to coloured light at different light intensities. When a relatively low light intensity was wanted, only the lamps mounted to the top of the light cabinet were used. The light intensity of such an irradiation is not quite comparable with the intensities obtained by irradiation from three sides.

The temperature during the experiments at higher intensities was 22° C during the photoperiod and 17° C during the dark period. In the experiments with low intensities the temperature was kept constant at 22° C.

Hyoscyamus niger

The results of experiments with light-grown plants have been given in the foregoing section (3.1.4) and showed that in red and in green light the plants remained in the rosette form. In blue light elongation occurred only in long days (16 hours of light per day), not in short days. The elongating effect of blue light is a long-day effect as it always was correlated with flower initiation.

The results of an experiment with dark-grown plants are given in Fig. 1. Immediately after sowing, pots with 25 seeds each were placed in 16R, 16G, or 16B. The intensity was 500 μW/cm². After 16 days the seedlings were selected for uniformity and 10 plants were left

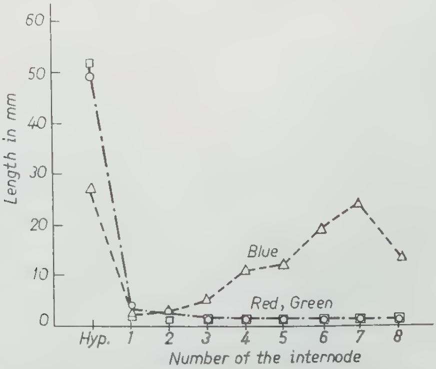

Fig. 1. The length of the hypocotyl and internodes of *Hyoscyamus niger*, sown in red, green or blue light. Irradiation 16 hrs per day. Light intensity 500 μW/cm². Day temperature 22° C. Night temperature 17° C. Length in mm, 60 days after sowing.

in each pot. At this time the hypocotyls were already completely developed. The length of the internodes was measured after 60 days. As can be seen the hypocotyls reached the same length in red and in green light but are much longer than those developed in blue light. The next internodes were very short in red and in green light, rosettes being formed. In blue light, however, after 2 or 3 short internodes elongation occurred. This elongation may have been caused by the long-day effect of 16B as all plants showed flower buds at this time. When germination had taken place in short days in blue light (10B) the internodes remained short and a rosette was formed.

Similar experiments with dark-grown seedlings were carried out at low light intensities, the plants being irradiated only from above. Three different light intensities were obtained by using gauze filters: 25, 120 and 210 μW/cm². A control was kept in darkness at the same temperature, 22° C. As can be seen in table 22 the hypocotyls of the plants grown in red, green or blue light of low intensity reached about the same length. In white light the seedlings were somewhat shorter than in coloured light.

TABLE 22

The influence of the light quality at low intensities on the elongation of the hypocotyl of *Hyoscyamus niger* sown in coloured light. Temperature 22° C. Length in mm, 38 days after sowing.

Light treatment in hrs per day	Light intensity in μW/cm²			
	0	25	120	210
16 red		38	31	28
16 green		40	34	32
16 blue		39	33	31
16 white		34	25	22
dark control	54			

Bean, "Vroege Wagenaar"

In preliminary experiments with bean plants it was found that light-grown seedlings reacted like gherkin seedlings in that in blue light the hypocotyl and the internodes were longer than in red or in green light. When the plants were sown in coloured light, however, the hypocotyls of plants grown in red or in green light were longer than of those grown in blue light.

In the following experiment the difference between light-grown and dark-grown seedlings is clearly shown. Seeds were sown in pots and left to germinate in continuous white fluorescent light (3200 μW/cm²). After 11, 9, 7 and 5 days, pots were transferred to the light cabinets. The plants were irradiated daily during 16 hours with red, green or blue light (475 μW/cm²). Each 3 or 4 days the length was determined; about 20 days after sowing the treatment was discontinued. At that moment the development of the hypocotyls and the first two internodes was completed. It was found that the hypocotyls and internodes which had first been exposed to white light became longer in blue than in red or green light, as far as they had not already finished development when the treatment with coloured light started. Those internodes which developed later, and for that reason had never been exposed to white light, were longer in red and green than in blue light.

In Fig. 2 the data are given of the development of the second internodes of plants sown 9 days (group II) and 5 days (group IV) and grown in white light before being transferred to the light cabinets.

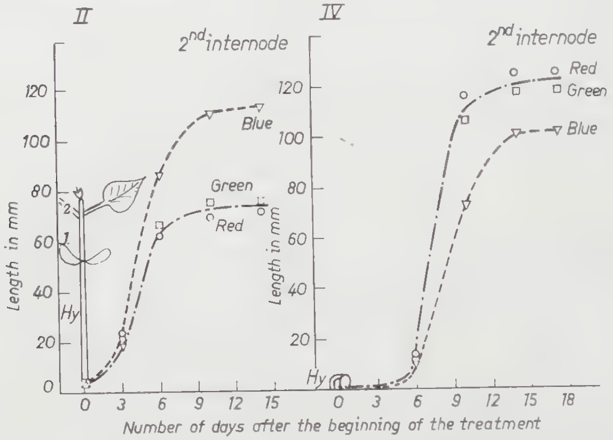

Fig. 2. The elongation of the second internode of bean plants grown in 16 hrs per day red, green or blue light (475 μW/cm²) as influenced by a previous irradiation with white light. II: irradiation with coloured light started 9 days after sowing; IV: idem 5 days after sowing. The initial lengths of the plants are given at 0. Day temperature 22° C, night temperature 17° C.

The second internode of seedlings of group II started to develop at the beginning of the treatment (0 days). In this case longer internodes were obtained in blue than in red or green light. Although the seedlings of group IV just came above the soil surface, the influence of the white light was notable, the hypocotyls being more elongated in blue light (128 mm) than in red light (105 mm). The second internode had not been affected by the white light so that they became longer in red than in blue light.

At very low light intensities, however, it was found that the elongation of the hypocotyls of seedlings sown in coloured light was much more inhibited in red than in blue light. The seeds were sown in red, blue or white (fluorescent) light and irradiated 16 hours per day. The light came only from above and by means of gauze filters three different light intensities were obtained. The temperature was kept constant at 22° C. After 11 days the treatment was discontinued as it was found that the hypocotyls did not develop any further. The results are given in Table 23.

The influence of the light intensity on the elongation was demonstrated in similar experiments but with higher intensities. The seeds were sown in red, blue or white light and irradiated 16 hours per day.

By means of gauze filters three light intensities were obtained. The day temperature was 22° C, the night temperature 17° C. 15 days after sowing, the elongation of the hypocotyls was completed. The results are given in Fig. 3.

TABLE 23

The influence of the light quality at low intensities on the elongation of the hypocotyl of bean seedlings sown in red, blue and white light. Temperature 22° C. Length in mm, 11 days after sowing.

Light treatment in hrs per day	Light intensity in μW/cm²			
	0	25	120	210
16 red		143	127	126
16 blue		179	173	157
16 white		161	136	127
dark control	253			

It is obvious that the inhibiting effect of red and blue light on the elongation of the hypocotyl depends on the light intensity. At higher intensities (about 750 μW/cm²) blue light is more active in this respect than red light. With decreasing light intensity the differences in length between plants grown in red or in blue light also decrease and at a certain intensity there is no difference at all. From the slope of the curves it may be expected that at lower intensities red light will be more inhibitive to elongation than blue light. This expectation is confirmed by the results obtained with experiments carried out with very low light intensities (see Table 23). In a certain intensity range

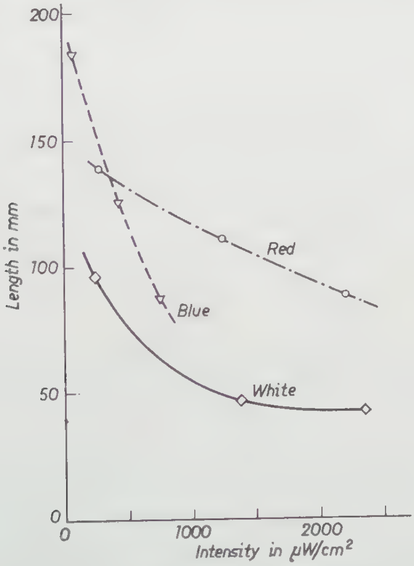

Fig. 3. The length of the hypocotyl of bean seedlings sown in red, blue and white light. Irradiation 16 hrs per day. Day temperature 22° C, night temperature 17° C. Length in mm, 15 days after sowing.

(200–700 μW/cm^2) the effect of white light is stronger than that of red or green light and at higher intensities it resembles that of blue light. At lower intensities it is between the effects of red and blue light.

Sinapis alba

Experiments with this plant species were carried out at high intensity and at low intensities (irradiated only from above). The plants were sown in pots immediately placed in the light cabinets. After 11 days the development of the hypocotyl was finished. The data are given in Table 24.

TABLE 24

The influence of the light intensity on the inhibiting effect of light on the elongation of the hypocotyl of *Sinapis alba* sown in light of different spectral regions; at high intensity (Experiment I), day temperature 22° C, night temperature 17° C; idem at low intensities (Experiment II), temperature 22° C. Length in mm, 11 days after sowing.

	Light intensity μW/cm^2	Light treatment (16 hrs per day)			
		red	green	blue	white
Exp. I	580	61	78	55	—
Exp. II	210	72	94	104	79
	120	70	98	109	86
	25	89	126	137	109
	0	180			

At 580 μW/cm^2 the hypocotyl of seedlings grown in blue light was shorter than that of seedlings in green and slightly shorter than that of the plants in red light (Experiment I). At the lower intensities it is obvious that even blue light is less active in inhibiting the elongation than red light. The activities of green and white light are between those of red and blue light.

Mirabilis jalapa

The effect of light of different wave-length regions on light-grown Mirabilis has already been given in Table 21. Younger internodes, which had not yet received white light before the treatment with coloured light started, reacted in the same way, the internodes of plants grown in blue light being shorter than in red and green light.

Also when the plants were sown in red or blue light (695 μW/cm^2) it was found that blue light was more active than red light in inhibiting elongation. However, at very low intensities (irradiation only from above) it was found that the difference in activity between blue and red light was much less pronounced, while at the lowest light intensity used (25 μW/cm^2) blue light was even less inhibitive than red light.

The results of two experiments with dark-grown seedlings are given in Table 25.

Tomato, "Victory"

In Table 21 it was shown that the hypocotyl of tomato plants, previously grown in white light, reached the same length in red, green or blue light and that the first internode of the same plants became longer in red or green light than in blue light.

TABLE 25

The influence of red and blue light on the elongation of *Mirabilis jalapa* sown in coloured light. Irradiated 16 hrs per day. Experiment I: at high intensity (695 μW/cm^2). Day temperature 22° C, night temperature 17° C. Length of hypocotyl and 1st internode in mm, 20 days after sowing. Experiment II: at low intensities, irradiated only from above. Temperature 22° C. Length of hypocotyl in mm, 18 days after sowing.

	Light intensity in μW/cm^2	Light treatment 16 hrs per day		
		red	blue	white
Experiment I				
hypocotyl	695	101	21	—
1st internode	695	133	47	—
Experiment II				
hypocotyl	210	97	88	80
	120	107	94	97
	25	102	122	104
	0	139		

In the following experiment the reactions of light-grown plants were compared to those of dark-grown seedlings. The light-grown plants were raised in white fluorescent light. After the hypocotyl had reached a length of about 30 mm, the seedlings were potted

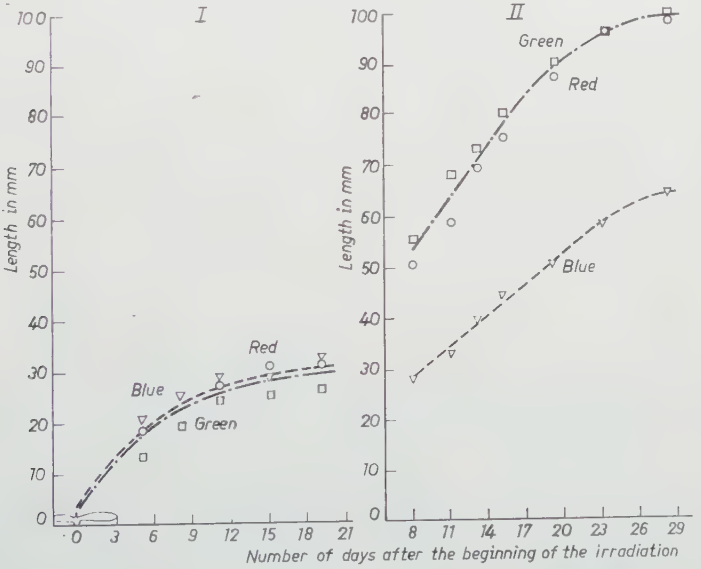

Fig. 4. The increase in length of the hypocotyls of tomato seedlings in red, green or blue light (475 μW/cm^2). Irradiation 16 hrs per day. Experiment I: seedlings germinated in white light and transferred to the light cabinets 13 days after sowing. Initial length of the hypocotyl about 30 mm. Experiment II: seedlings sown in the light cabinets. Day temperature 22° C, night temperature 17° C.

with the cotyledons on the soil surface. The next day, the plants were transferred to the light cabinets (Experiment I) .The dark-grown seedlings were sown immediately in the light cabinets (Experiment II). The plants were irradiated with red, green or blue light, 16 hours per day. The light intensity was 475 μW/cm^2. The day temperature was 22° C, the night temperature 17° C. The length of the hypocotyls was measured each 3 or 4 days. The increase in length of the hypocotyls of the light-grown plants, 30 mm being under the soil surface, and of the seedlings sown in coloured light is given in Fig. 4. The hypocotyls of plants germinated in white light reached the same length whether grown in red, green or blue light. The elongation of the hypocotyls of the seedlings sown in coloured light was much more inhibited in blue than in red or green light.

When different light intensities were compared it was found that only at very low light intensities (irradiation only from above) the difference in activity between blue and red light decreased with decreasing light intensity. In these experiments the plants were sown in red, blue or white light and irradiated 16 hours per day. The temperature was kept at 22° C. The results of one of these experiments are given in Fig. 5. At the lowest intensity, blue light was even less effective than red light in inhibiting the elongation of the hypocotyl.

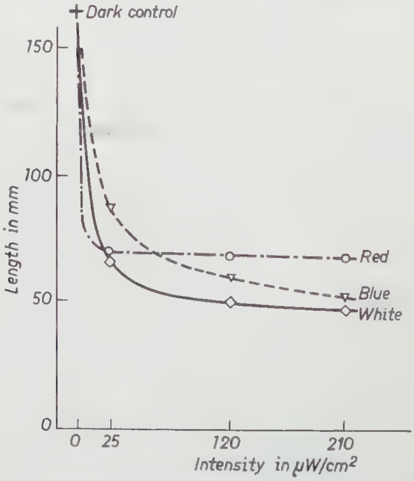

Fig. 5. The elongation of the hypocotyl of tomato seedlings sown in 16 hrs per day red, blue or white light of low intensities (irradiation only from above). Temperature 22° C. Length in mm, 16 days after sowing.

At the highest intensity the effect of white light resembled that of blue light, at the lowest intensity it was similar to that of red light. Evidently there is an intensity range in which white light is more active in inhibiting the elongation than red or blue light.

Gherkin, "Venlose niet-plekkers"

Gherkin seedlings, germinated in white light, later on developed longer hypocotyls and longer internodes in blue light than in red or green light (Table 21). When these seedlings were transferred to a dark room the hypocotyls developed until the same length was reached as occurred in red or green light.

Fig. 6 gives the results obtained from an experiment (I) with light-grown seedlings exposed to light of different qualities and low intensities. The lengths were measured 12 days after the beginning of the irradiation with 16 hours per day of red, blue or white light. The low light intensities were obtained by irradiating the plants only from above. The temperature was maintained at 22° C. It can be seen that with increasing light intensity the length of the hypocotyl of light-grown seedlings in blue light increases much more than in white or red light, in which elongation was about the same as in darkness. The initial length of the hypocotyls was 10 mm.

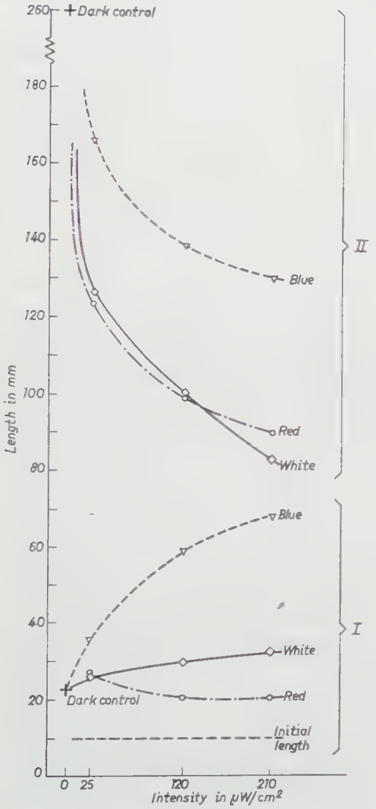

Fig. 6. The influence of red, blue or white light on the elongation of the hypocotyl of gherkin seedlings germinated in white light (I) and seedlings germinated in red, blue or white light (II). Irradiation 16 hrs per day with low light intensities (irradiation only from above). Temperature 22° C. Length in mm, 12 days (I) and 11 days (II) after the beginning of the exposure to coloured light. The length of the dark control in I is given after 7 days as the seedlings wilted and died quite soon afterwards.

If gherkin seedlings were sown, however, in the different light cabinets under the same conditions as in the foregoing experiment the elongation of the hypocotyl decreased with increasing light intensity. Blue light was the least active type of light in inhibiting the elongation, red and white light showed to be active to the same extent when the light intensity was low (Fig. 6, Experiment II).

In experiments with seedlings sown in darknesss and in red, blue or white light of higher intensities than used in the foregoing experiment, it was found that the difference between the activity of red and blue light in inhibiting the elongation decreases with increasing light intensity (Fig. 7). At a certain light intensity both red and blue light will inhibit the elongation to the same extent. From the slope of the curves it may even be expected that with intensities higher than were used, blue light will be more active than red light. Besides it is obvious that in a certain intensity range white light is more active than red or blue light of the same intensity.

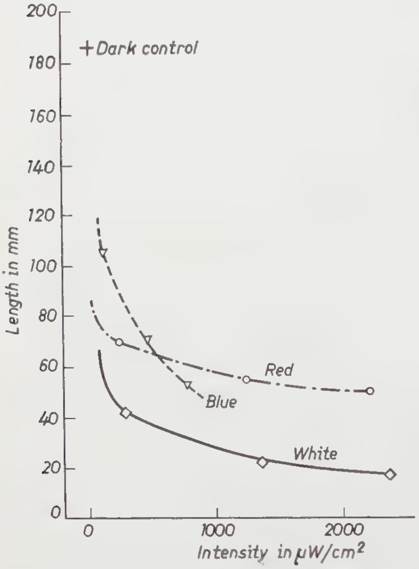

Fig. 7. The influence of the light intensity on the elongation of the hypocotyl of gherkin seedlings sown in darkness, red, blue or white light. Irradiation 16 hrs per day. Day temperature 22° C, night temperature 17° C. Length in mm, 11 days after sowing.

Thus the experiments described above clearly demonstrate that the difference between the inhibiting effects caused by light of different spectral regions does not depend on the plant species but on the light intensity used. The difference between the plant species is that they are not equally sensitive to light of a certain intensity.

3.2.3 Light-grown plants in continuous darkness

Plants completely grown in darkness show an excessive elongation which can be inhibited by very small amounts of light. When seedlings germinated in white light were transferred to darkness, however, it was often noted that hardly any additional elongation occurred. In the case of gherkin seedlings this difference between dark-grown and light-grown seedlings is clearly shown in Fig. 6 (+). The same difference was obtained with tomato plants.

Using light-grown gherkin seedlings it appeared that in blue light the elongation was stimulated (Fig. 6, I). The elongation of seedlings not exposed to white light before was inhibited by blue light. The light-grown seedlings died some time after being exposed to darkness or to 25 μW/cm^2 of blue light while seedlings sown in darkness or in blue light (25 μW/cm^2) still continued growth. To study this effect the following experiment was carried out.

The light-grown gherkin seedlings were transferred to continuous darkness. The temperature was maintained at 22° C. Of one group of seedlings, one cotyledon was continuously soaked in a vessel containing water or a 5 % sucrose solution. The results of three experiments are given in Table 26. The length was measured 8 days after the beginning of the treatment. From these data it is obvious that the slight elongation in darkness—the initial length was 10 mm—was not caused by any after-effect of the previous irradiation with white light, but probably to a lack of photosynthates as a supply of sucrose caused a marked elongation. Similar results were obtained with light-grown tomato plants exposed to continuous darkness with or without a sucrose supply.

TABLE 26

The elongation of the hypocotyl of light-grown gherkin seedlings in continuous darkness without or with one cotyledon continuously soaked in water or a 5 % sucrose solution. Temperature 22° C. Length in mm, 8 days after the beginning of the dark treatment.

Treatment	Experiment		
	I	II	III
Control	32	35	20
Water	29	—	20
5 % sucrose	107	103	110

Light-grown gherkin seedlings transferred to darkness or to red light elongate to about the same extent. As photosynthesis takes place in red light, it is obvious that the slight elongation in red light is not caused by a lack of photosynthates but may be due to an inhibiting effect of red light on the elongation. In blue light the hypocotyls elongate to a much larger extent, photosynthates are also formed, the higher the intensity the more photosynthesis. Besides, blue light in this intensity range is much less effective in inhibiting the elongation than red light. All this accounts for the fact that elongation in blue light increased with increasing light intensity (Fig. 6, I). The results of the following experiment support this assumption.

Light-grown gherkin seedlings were exposed to continuous darkness or irradiated with red or blue light, 16 hours per day. One part of each group was treated with sucrose by immersing one cotyledon in a vessel containing a 5 % solution of this carbohydrate. The light intensity was 640 μW/cm^2. The temperature was maintained at 22° C. The length of the hypocotyls was measured 7 days after the beginning of the treatment. From the data, presented in Table 27 it can be seen that a sugar supply to plants grown in red or in blue light did hardly influence the elongation.

TABLE 27

The elongation of the hypocotyl of light-grown gherkin seedlings in darkness, red or blue light (640 μW/cm^2) without or with one cotyledon continuously soaked in a 5 % sucrose solution. Irradiation 16 hrs per day. Temperature 22° C. Length in mm, 8 days after the beginning of the treatment.

Spectral region	Control	5 % sucrose
Red	37	46
Blue.	88	93
Dark control	25	101

3.2.4 ANTAGONISM BETWEEN LIGHT OF DIFFERENT SPECTRAL REGIONS

In a previous paper (MEIJER 1958*a*) it has already been reported that blue light has not only an inhibiting effect but can also promote the elongation of already inhibited internodes. This was concluded from experiments in which light-grown gherkin seedlings were exposed to 8 hours of red light per day (600 μW/cm^2). Some of the plants were kept in darkness during the remaining 16 hours (8R), other groups were exposed to 8 hours of supplemental blue light of three different intensities and afterwards kept in darkness for the remaining 8 hours (8R 8B). The results are listed in Table 28. Plants exposed to 16 hours of red light are even somewhat shorter than those exposed to 8 hours of red light. The elongating effect of blue light cannot be due to a larger production of photosynthates than in the case of plants which did not receive supplemental light, a sugar supply being virtually ineffective in the latter case (Table 27).

TABLE 28

The influence of 8 hrs blue light (I) and of 10 minutes near infra-red radiation (II) supplementarily given after 8 hrs red light (600 μW/cm^2), on the elongation of the hypocotyl of light-grown gherkin seedlings. Length in mm, 7 (I) and 8 (II) days after the beginning of the treatment.

Light treatment	I		II	
	Blue light μW/cm^2	Length in mm	Near infra-red μW/cm^2	Length in mm
8R	0	23	0	39
8R8B	60	52		
8R8B	300	75		
8R8B	600	79		
8R10′IR			200	104

With near infra-red radiation the same effect was obtained as with blue light. Light-grown gherkin seedlings were exposed to 8 hours of red light per day (670 μW/cm^2). Some of the plants were irradiated immediately afterwards with 10 minutes of near infra-red (obtained from a neon lamp). The intensity of this radiation was 200 μW/cm^2. The temperature during the day and the first 8 hours of the dark period was 22° C, during the second 8 hours 17° C. After 8 days the treatment was discontinued and the length measured in mm (Table 28).

From these results it is obvious that both near infra-red and blue radiation are active in antagonizing the inhibiting effect of red light.

3.2.5 Discussion

1. *Plant species*

In a previous paper (Meijer 1957*b*) it was suggested that the spectral region which is most active in inhibiting the elongation of internodes, may vary with the plant species. In Table 21 (p. 225) the results were given of experiments with several plant species exposed to light of different spectral regions. In all these experiments the plants had grown before in white light and the other conditions were the same. These results show that, as far as the activity of red and blue light on the elongation is concerned, there are two extreme types of plants:

1° the “Mirabilis type”: inhibition by blue light more pronounced than by red light;
2° the “Gherkin type”: red light more inhibitive than blue light.

This distinction between the two types can only be indicative because the differences between the inhibiting effects of red and blue light are quantitatively not always the same; there also exist plants which stand between these two types. Vince (1956) also concluded from her experiments with Pisum and tomato that the difference in response may be due to the plant species.

2. *Light intensities*

The experiments carried out with different light intensities demonstrate, however, that it depends on the light intensity and not on the

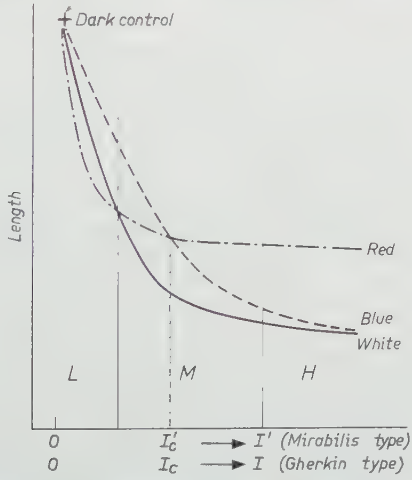

Fig. 8. The elongation of an internode in red, blue or white light as a function of the light intensity. The intensity scale of the “Mirabilis type” (I') is different from that of the “Gherkin type” (I) : $I > I'$. I_c and I'_c are the “critical intensities”. L, M and H are the relatively low, the medium and the high intensity zones. (A schematical representation of the results of the experiments described in 3.2.2).

plant species whether blue light or red light is most effective in inhibiting the elongation of internodes. It was found with plants of the two types that at relatively high light intensities blue light is more active than red light, whereas at relatively low light intensities the situation is reversed.

Evidently there must exist a certain "critical intensity" at which the elongation of the internodes of plants exposed to red and of those exposed to blue light will be inhibited to the same extent, i.e. at which the internodes will reach the same length. This is clearly demonstrated in Figs. 3 ,5 and 7 and also in Table 22. Now the value of this "critical intensity" depends on the plant species: with plants of the "Mirabilis type" e.g. tomato, *Mirabilis* and *Hyoscyamus* it is reached at low light intensities, but in the case of plants of the "Gherkin type", e.g. gherkin, bean and *Petunia*, it is found at much higher light intensities.

The elongation of an internode as a function of the light intensity is schematically given in Fig. 8 for red, blue and white light. In this figure I_c and I'_c represent the "critical intensity". The intensity scale for the Mirabilis type, I′, is more extended than that for the "Gherkin type", I.

3. *Two photoreactions*

a. Difference in activity

Possibly at low intensities (Fig. 8, zone L) only one photoreaction is involved in inhibiting the elongation of internodes, which is more sensitive to red than to blue light. This photoreaction will be saturated with red light at a lower intensity than with blue light.

It was found, however, that the blue light curve does not only appraoch the red light curve but even crosses it (I_c). When the blue light reaction approaches saturation (zone H), blue light is even more effective than red light. This can only be explained by assuming that two different photoreactions are involved in the process inhibitive to the elongation, one photoreaction being sensitive to red light, the other to blue light. The blue light reaction increases less with increasing intensity and is saturated at a higher intensity than the red light reaction, but the inhibition caused by the blue light reaction at saturation intensity is stronger than that caused by the red light reaction.

b. Interaction

It has been reported that a combination of red and blue light is more inhibitive than an addition of the effects of each type of light (MEIJER 1958*a*). Gherkin seedlings were left to germinate in darkness. When a certain length was reached two groups of plants were exposed to blue (B) and two groups to red light (R). The light intensity was 310 $\mu W/cm^2$. After two days one group of plants irradiated with blue light was transferred to red light (B → R) and one group previously exposed to red light was transferred to blue light (R → B). The increase in length of plants exposed to blue light only was about 80 mm and of those exposed to red light only 60 mm. The plants which received two days of blue light before the exposure to red light (B → R), however, were much more inhibited than the other groups, the increase in length being only 30 mm. On the other hand, blue light after red light (R → B) had almost the same effect as red light alone. These results too give an indication that blue and red light are involved in two different photoreactions, the red sensitive reaction being much more pronounced after blue or white light than without such a pretreatment.

This interaction between red and blue light may also be the cause of light-grown gherkin seedlings being much more inhibited in red light than seedlings sown in red light of the same intensity. In blue light, dark-grown and light-grown gherkin seedlings reached about the same height.

4. *White light*

It was calculated from its emission spectrum that white fluorescent light contains about 25 % blue radiation ($\lambda = 4000$–5000 Å) and 75 % green and red radiation ($\lambda = 5000$–7000 Å). Although the results with green light are not discussed in this paper it may be mentioned here that this light quality is active in a similar way as, but to a lesser extent than red light.

In case both the blue light reaction and the red light reaction become stronger with increasing light intensity, it is obvious that the activity of white light will be intermediary between the activity of red and of blue light (Fig. 8, zone L).

When the red light reaction is more or less saturated, the blue light reaction still becomes stronger with increasing light intensity. For that reason, at moderate intensities white light is even more active than red or blue light in inhibiting the elongation (zone M).

At still higher intensities (zone H) the blue photoreaction, too, approaches saturation and with it the reaction to white light.

5. *Antagonism*

Experiments with light-grown gherkin seedlings showed that, in addition to this inhibiting effect blue light also has an antagonizing effect on the inhibition by red light (Table 28). The inhibition caused by a previous red irradiation will be antagonized only to a certain extent. This elongating effect of blue light was not found with some other plants species; possibly the light intensities were sufficiently high for the inhibiting activity to dominate the antagonizing activity. So the ultimate result will depend on an equilibrium between both activities.

A similar dual rôle as mentioned for blue light, has been reported for near infra-red radiation (De Lint 1957). Near infra-red was found to inhibit the elongation of dark-grown seedlings (Withrow 1941; De Lint 1957). On the other hand the inhibition of the elongation by light can be reversed partly by subsequently exposing the plants to near infra-red immediately after the irradiation which caused the inhibition (Hendricks *et al.* 1956; Downs *et al.* 1957; De Lint 1957). The extent to which near infra-red reverses the inhibition caused by a previous irradiation depends on its own inhibiting action.

This antagonizing effect of near infra-red is also shown in the present paper (Table 21). In these experiments exposure to near infra-red was simultaneous with exposure to the visible, inhibitive, radiation. Exposure together with red light had hardly any or no effect. This may be explained by the reversibly antagonizing effects of both spectral regions (Borthwick *et al.* 1952*b*). Simultaneously given with green light, near infra-red caused elongation (i.e. reversed the inhibiting effect of the visible radiation) only at those intensities in which blue light was less effective than red light (zone L), e.g. gherkin, *Salvia* and tomato (hypocotyl). When red light was less effective than blue light (zone H) no influence was found e.g. *Mirabilis* and tomato (first internode). The same is valid for near infra-red given simultaneously with blue light (Table 21).

6. *Photosynthesis*

The method used in our experiments of growing plants in coloured light has the advantage that the plants can be exposed to a large amount of light. The disadvantage is the difference between the photosynthetic rates of plants grown in red light and of those grown in blue light. It was found that the dry weight of plants grown in red light is higher than that of plants grown in blue light. This was valid for all the light intensities investigated (zones L, M and H). Therefore a difference in photosynthesis cannot be of primary importance. It was reported (Table 27) that sucrose supplied to plants grown in red and blue light did not markedly change the difference in activity between these two light qualities. Similar results have been reported by Vince (1956).

Batalin (1871) and Trumpf (1924) have concluded that the excessive elongation in darkness is not caused by the absence of photosynthesis because it was possible to obtain plants without chlorophyll by a brief exposure to light of a high intensity. These plants had a shape similar to that of normal light-grown plants. It was also shown that albino and potentially green barley seedlings have the same action spectrum for elongation (Borthwick *et al.* 1951). Another indication that the inhibition of elongation is not correlated with photosyntheses or even with the chlorophyll content was given by Withrow (1941) and Klein *et al.* (1957).

7. *Light-grown plants*

Wassink *et al.* (1956) concluded that light-grown plants and dark-grown seedlings react in a different way. In the case of the former red light would be the most active type of light but with the latter blue light would be most active in inhibiting the elongation. In this paper, however, it has been shown that, depending on the intensity, blue light can be the most active light in inhibiting the elongation of dark-grown seedlings. With light-grown plants it was shown that blue light is sometimes less effective than red light.

It is possible that the "critical intensity" of light-grown plants has a higher value than that of dark-grown plants. It was found that at the same light intensity blue light was more active than red light when dark-grown seedlings were used. If, on the other hand, light-grown seedlings were exposed to blue and red light of the same intensity, it was shown that red light was the most effective in inhibiting the elongation (Fig. 2). Apparently this difference between light-grown plants and dark-grown seedlings is only a quantitative difference instead of a qualitative one.

Another difference was found in the reaction to continuous darkness. It was noted that light-grown plants (gherkin, tomato) hardly elongate while exposed to darkness. When, however, sucrose was supplied, a remarkable elongation was obtained. Similar results have been acquired with pea stem sections of light-grown seedlings, kept in darkness (Galston *et al.* 1951).

8. *Auxin*

It has been assumed that both the blue light reaction and the red light reaction are involved into different processes, leading to the same ultimate result e.g. a decrease of the auxin content (Meijer 1958*b*). Although this assumption is quite tentative several indications where obtained that the auxin metabolism is influenced by light.

a. First of all Galston *et al.* (1949) demonstrated that indole-acetic acid, which is a natural auxin, can be photo-oxidized by blue light in the presence of riboflavine. The inhibiting effect of blue light on elongation may be caused by this IAA-inactivation.

b. It is possible that near infra-red and blue light, too, increase the auxin content (Meijer 1958*b*). When young tomato plants, raised in white light, were exposed to green + near infra-red, a strong epinastic curvature of the leaves occurred within about four hours and disappeared after about 48 hours. Almost immediately the internodes started elongation. The epinastic curvature was exactly the same as was obtained in white light with plants sprayed with an IAA-solution. In blue light this epinasty was also found although to a lesser extent, however, no elongation of the internodes occurred. In red or green light this phenomenon was not noted at all. When the plants in green + near infra-red were pretreated with an anti-auxin like coumarin or penta-chlorophenoxy-acetic acid, the epinasty as well as the subsequent elongation was prevented.

c. In the same paper it was reported that the elongation of gherkin seedlings in red or green light and even the much stronger elongation in green + near infra-red or in blue light, was stimulated after an application of auxins. It was remarkable that indole-acetic acid was less effective than the other indole compounds used, such as tryptophol or tryptamine.

This auxin-induced elongation of light-grown gherkin seedlings but also the elongation caused by blue light was prevented when an anti-auxin was supplied. It might be mentioned here that the development of the plants was normal as no injurious effect was obtained.

d. The following phenomenon also gives an indication that near infra-red or blue light may increase the auxin content (MEIJER 1958*b*). When light-grown gherkin seedlings were transferred to continuous darkness after a previous exposure to 16 hours of blue light or near infra-red, almost all plants drooped down on the fifth day in darkness. Just before this occurred, it was found that in a region about 10 mm below the insertion of the cotyledons small droplets appeared on the epidermis, which was followed by a loss of turgor in this zone causing the seedlings to droop. The other parts of the seedlings were still completely turgescent, but wilted quite soon afterwards. This phenomenon was not observed, however, if the plants were pre-illuminated with red light instead of blue or near infra-red radiation. When the seedlings previously exposed to red light were also treated with an auxin, exactly the same drooping effect was obtained as with plants previously exposed to blue or near infra-red.

It is obvious therefore that certain phenomena induced by blue or near infra-red can also be obtained with an auxin treatment.

Evidently the auxin content is influenced by light. Blue light causes a photo-oxidation of the indole-acetic acid in the presence of riboflavine. Red light may also decrease the auxin content, but this process will be different from the blue-light reaction. It may be that either IAA is inactivated in a different way or that the production of IAA is inhibited. This process can be reversed by blue and near infra-red, as far as (in the case of blue light) the photo-oxidizing activity does not dominate. BLAAUW–JANSEN (1959) has shown that the auxin content decreases after an irradiation with red light.

It is to be expected, that the inhibition of the elongation is much more complicated than can be concluded from the results of our experiments. HILLMAN *et al.* (1957) reported that red light decreases the activity of indole-acetic-acid oxidase which will result in a higher auxin content. This process is reversed by an exposure to near infra-red and this reversal will cause a decrease of the auxin content. These results do not agree with our experiments in which indications were found that near infra-red may cause an increase of the auxin content. GOLDACRE *et al.* (1953) found that the indole-acetic-acid oxidase activity of extracts of pea epicotyls was much higher when the plants were grown under continuous red light than in darkness.

The response of the plant to auxin may also be influenced by light, the sensitivity to auxin was reported either to be increased (KENT *et al.* 1951, LIVERMAN *et al.* 1953) or to be reduced (GALSTON *et al.* 1953, KLEIN *et al.* 1956) by red light. Recently BLAAUW–JANSEN (1959), in her experiments on phototropism, found a "red light factor" which enhances the effect of blue light and of IAA at low concentrations on the *Avena* coleoptile. It was found that gibberellic acid had a similar effect as red light in this respect.

9. *Conclusion*

Several authors reported results of experiments concerning the influence of the amount of light on the elongation. Åberg (1943) suggested the light intensity to determine which spectral region would be most active in inhibiting the elongation. Our experiments confirm this suggestion.

In those investigations in which it was found that red light was more effective in inhibiting the elongation than blue light, the "critical intensity" might not have been reached yet. In the other investigations in which blue light appeared to be more effective than red light, the intensities used might have been always higher than the "critical intensity". Obviously the conclusion that the difference in response to red and blue light does not depend on the light intensity but on the plant species (Vince 1956; — *et al.* 1957; Meijer 1957*b*; Van der Veen 1958) might be explained by assuming that in the experiments of Vince the differences between the intensities were too small. For *Pisum* the intensities of red and blue light may have been both in zone L, for tomato in zone H.

4. SUMMARY

4.1 *Photoperiodism*

The influence of light of different spectral regions on the long-day effect was studied on several plant species, with special reference to *Salvia occidentalis* (SDP).

I. A long-day effect was obtained by means of:
  1° a long-day treatment in coloured light; near infra-red and blue light appeared to be the most active spectral regions;
  2° a nightbreak treatment in coloured light; the requirement was found that the main light period had to contain blue of near infra-red; red light showed to be the most active nightbreak light;
  3° a supplemental light treatment in coloured light; the same spectral dependence for the main light period was found as in 2°, blue light was more active as supplemental light than red light.

II. It was demonstrated that:
  1° the effect of near infra-red and blue light (main-light-period reaction) could be counteracted by red light;
  2° the effect of red light (nightbreak reaction) could be reversed by near infra-red or blue light;
  3° the inactivity of red supplemental light (low intensity) was only seeming, it was caused by the antagonizing effect of red light on the main-light-period reaction induced by blue light (II, 1°).

III. It was concluded that it depends on the interaction of two photoreactions and not on the daylength whether a long-day effect is obtained or not; under certain conditions these reactions will even take place within short photoperiods (short days).

4.2 *Elongation*

The influence of light of different spectral regions on the elongation of various plant species was studied.

1° It depends on the light intensity whether red light is more active than blue light or, conversely blue light is more active than red light, in inhibiting the elongation of internodes.

2° At relatively low intensities red light is the most active type of light; at relatively high intensities blue light is more active than red light. This implies that at a certain intensity ("critical intensity") red and blue light are equally effective.

3° The value of the critical intensity depends on the plant species used. For plants belonging to the "Mirabilis type" the value of the "critical intensity" is lower than in the case of plants belonging to the "Gherkin type".

4° In addition to an inhibiting activity, blue light also has an antagonizing effect on the inhibition caused by red light ("dual rôle").

5° The results are briefly discussed in connection with a possible influence on the auxin content.

6° Just as in photoperiodism (II, 2°) the effect of red light can be reversed by near infra-red or blue radiation.

ACKNOWLEDGEMENT

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REFERENCES

Åberg, B. 1943. Symb. Bot. Upsal. **8** (1): 1.
Batalin, A. 1871. Bot. Zeitung **29**: 669.
Blaauw–Jansen, G. 1959. Acta Bot. Neerl. **8**: 1 (thesis).
Bonner, J. and J. Liverman. 1953. in W. E. Loomis: Growth and differentiation of plants (Iowa State Coll. Press).
Borgström, G. 1939. Bot. Not.: 830.
Borthwick, H. A., S. B. Hendricks and M. W. Parker. 1948. Bot. Gaz. **110**: 103.
———, ——— and ———. 1951. Bot. Gaz. **113**: 95.
———, ———, ———, E. H. Toole and V. K. Toole. 1952*a*. Proc. Nat. Acad. Sci. **38**: 662.
———, ——— and ———. 1952*b*. Proc. Nat. Acad. Sci. **38**: 929.
———, ———, E. H. Toole and V. K. Toole. 1954. Bot. Gaz. **115**: 205.
Bünning, E. 1958. Die physiologische Uhr (Springer Verlag).
Buy, H. G. du and E. Nuernbergk. 1930. Proc. Kon. Akad. Wetensch. **33**: 542.
Cathey, H. M. and H. A. Borthwick. 1957. Bot. Gaz. **119**: 71.
Currey, G. M. and E. C. Wassink. 1956. Med. Landb. Hogeschool Wageningen **56**: 1.
Downs, R. J. 1955. Plant Phys. **30**: 468.
———. 1956. Plant Phys. **31**: 279.
———, S. B. Hendricks and H. A. Borthwick. 1957. Bot. Gaz. **118**: 199.
Fife, J. M. and Ch. Price. 1953. Plant Phys. **28**: 475.
Flint, L. H. and E. D. McAlister. 1935. Smithsonian Inst. Publs. Misc. Coll. **94** (5): 1
Funke, G. L. 1944. De formatieve invloed van het licht op planten (Noorduyn & Zoon – Gorinchem).
———. 1948. in A. E. Murneek and R. O. Whyte: Vernalization and Photoperiodism (Chron. Bot. Comp.).
Galston, A. W. and R. S. Baker. 1949. Am. Journ. Bot. **36**: 773.
——— and ———. 1951. Plant Physiol. **26**: 311.
——— and ———. 1953. Am. Journ. Bot. **40**: 512.
Goldacre, P. L., A. W. Galston and R. L. Weintraub. 1953. Arch. Biochem. Biophys. **43**: 358.
Hamner, K. C. 1940. Bot. Gaz. **101**: 658.
Haupt, W. 1948. Naturw. **45**: 273.
Hendricks, S. B., H. A. Borthwick and R. J. Downs. 1956. Proc. Nat. Acad. Sci. **42**: 19.
Hillman, W. S. 1957. Science **126**: 165.
——— and A. W. Galston. 1957. Plant Phys **32**: 129.
Jones, M. B. and L. F. Bailey. 1956. Plant Phys. **31**: 447.
Kent, M. and W. A. Gortner. 1951. Bot. Gaz. **112**: 307.

Klein, W. H., R. B. Withrow and V. Elstad. 1956. Plant Phys. **31**: 289.
———, ———, ——— and L. Price. 1957. Am. Journ. Bot. **44**: 15.
Könitz, W. 1958. Planta **51**: 1.
Koningsberger, V. J. 1922. Rec. trav. bot. néerl. **19**: 1.
Lang, A. and G. Melchers. 1943. Planta **33**: 653.
Leopold, A. C. 1949. Plant Phys. **24**: 530
———. 1952. Am. Journ. Bot. **40**: 46.
Lint, P. J. A. L. de. 1957. Med. Landb. Hogeschool Wageningen **57**: 1.
Liverman, J. L. and J. Bonner. 1953. Proc. Nat. Acad. Sci. **39**: 905.
———, M. P. Johnson and L. Starr. 1955. Science **121**: 440.
Lörcher, L. 1958. Zeitschr. f. Bot. **46**: 209.
Meijer, G. 1957*a*. Acta Bot. Neerl. **6**: 395.
———. 1957*b*. Symp. on photoperiodism and related phenomena. Gatlinburg. Tenn. (in press).
———. 1958*a*. Acta Bot. Neerl. **7**: 614.
———. 1958*b*. Acta Bot. Neerl. **7**: 621.
——— and R. van der Veen. 1957. Acta Bot. Neerl. **6**: 429.
Mohr, H. 1956. Planta **46**: 534.
———. 1957. Planta **49**: 389.
Parker, M. W., S. B. Hendricks, H. A. Borthwick and N. J. Scully. 1946. Bot. Gaz. **108**: 1.
———. ———, ——— and F. W. Went. 1949. Am. Journ. Bot. **36**: 194.
———, ——— and ———. 1950. Bot. Gaz. **111**: 242.
Piringer, A A. and P. H. Heinze. 1954. Plant Phys. **29**: 467.
Popp, H. W. 1926. Am. Journ. Bot. **13**: 706.
Rasumov, V. I. 1933. Bull. Appl. Bot. Leningrad III, **3**: 217.
Roodenburg, J. W. M. 1940. Rec. trav. bot. néerl. **27**: 301.
———. 1954. Rapp. Huitième Int. Bot. Paris Sect. 11 et 12: 318.
Shirley, H. L. 1929. Am. Journ. Bot. **16**: 354.
Siegelman, H. W. and S. B. Hendricks. 1957. Plant Phys. **32**: 393.
Stolwijk, J. A. J. 1952. Proc. Kon. Ned. Akad. Wetensch. **C 55**: 489.
———. 1954. Med. Landb. Hogeschool Wageningen **54**: 181 (thesis).
——— and J. A. D. Zeevaart. 1955. Proc. Kon. Ned. Akad. Wetensch **C 58**: 386
Takimoto, A. 1957. Bot. Mag. Tokyo **70**: 321.
Tashima, Y. 1953. Proc. Japan Acad. **29**: 271.
——— and S. Imamura. 1953. Proc. Japan Acad. **29**: 581.
Toole, E. H., V. K. Toole, H. A. Borthwick and S. B. Hendricks. 1955. Plant Phys. **30**: 15.
Trumpf, C. 1924. Bot. Arch. **5**: 381.
Veen, R. van der. 1950. Philips Techn. Rev. **12**: 1.
———. 1958. Sci. Hort. **13**: 33.
——— and G. Meijer. 1958. Licht und Pflanzen (Philips Technische Bibliotheek).
Vince, D. 1956. Journ. Hort. Sci. **31**: 16.
——— and R. H. Stoughton. 1957. in J. P. Hudson: Control of the plant environment, p. 72 (Butterworths, London).
Wallrabe, E. 1944. Bot. Arch. **45**: 281.
Wareing, P. F. and M. Black. 1958. Nature **181**: 1420.
Wassink, E. C., C. M. J. Sluysmans and J. A. J. Stolwijk. 1950. Proc. Kon. Ned. Akad. Wetensch. **53**: 1466.
———, J. A. J. Stolwijk and A. B. R. Beemster. 1951. Proc. Kon. Ned. Akad. Wetensch. **C 54**: 421.
——— and ———. 1952. Proc. Kon. Ned. Akad. Wetensch. **C 55**: 471.
——— and ———. 1956. Ann. Rev. Plant Phys. **7**: 373.
———, J. Bensink and P. J. A. L. de Lint. 1957. 2nd Intern. Photobiol. Congress.
———, P. J. A. L. de Lint and J. Bensink. 1957. Symp. on photoperiodism and related phenomena. Gatlinburg, Tenn. (in press).
Weintraub, R. L. and L. Price. 1947. Smithsonian Inst. Publs. Misc. Coll. **106** (21): 1.
Went, F. W. 1941. Am. Journ. Bot. **28**: 83.

WITHROW, R. B. 1941. Plant Phys. **16**: 241.
——— and H. M. BENEDICT. 1936*a*. Plant Phys. **11**: 225.
——— and J. P. BIEBEL. 1936*b*. Plant Phys. **11**: 807.
——— and A. P. WITHROW. 1940. Plant Phys. **15**: 609.
———, J. B. WOLFF and L. PRICE. 1956. Plant Phys. **31**: XIII.
ZEEUW, D. DE. 1953. Proc. Kon. Ned. Akad. Wetensch. **C 56**: 418.

Plate 1 and 2. Photoperiodic response of Salvia occidentalis to light of different spectral regions.

The numbers of the corresponding Tables are given in brackets.

🟥 =red light; 🟩 =green light; 🟦 =blue light; ⬛ =near infra-red (broken lines: low intensity light.)

Short-day effect: +; long-day effect: —; long-day effect (partly): (—)

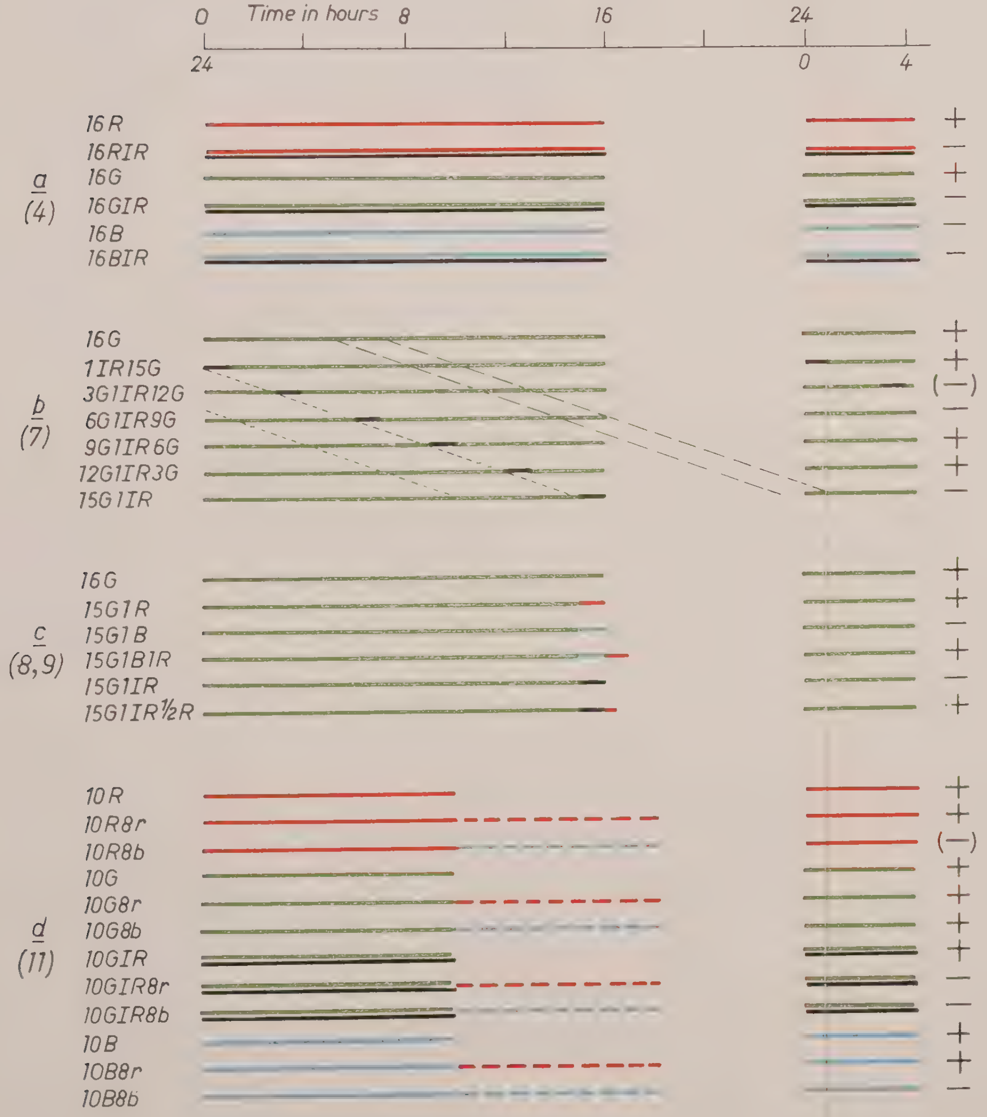

Plate 1

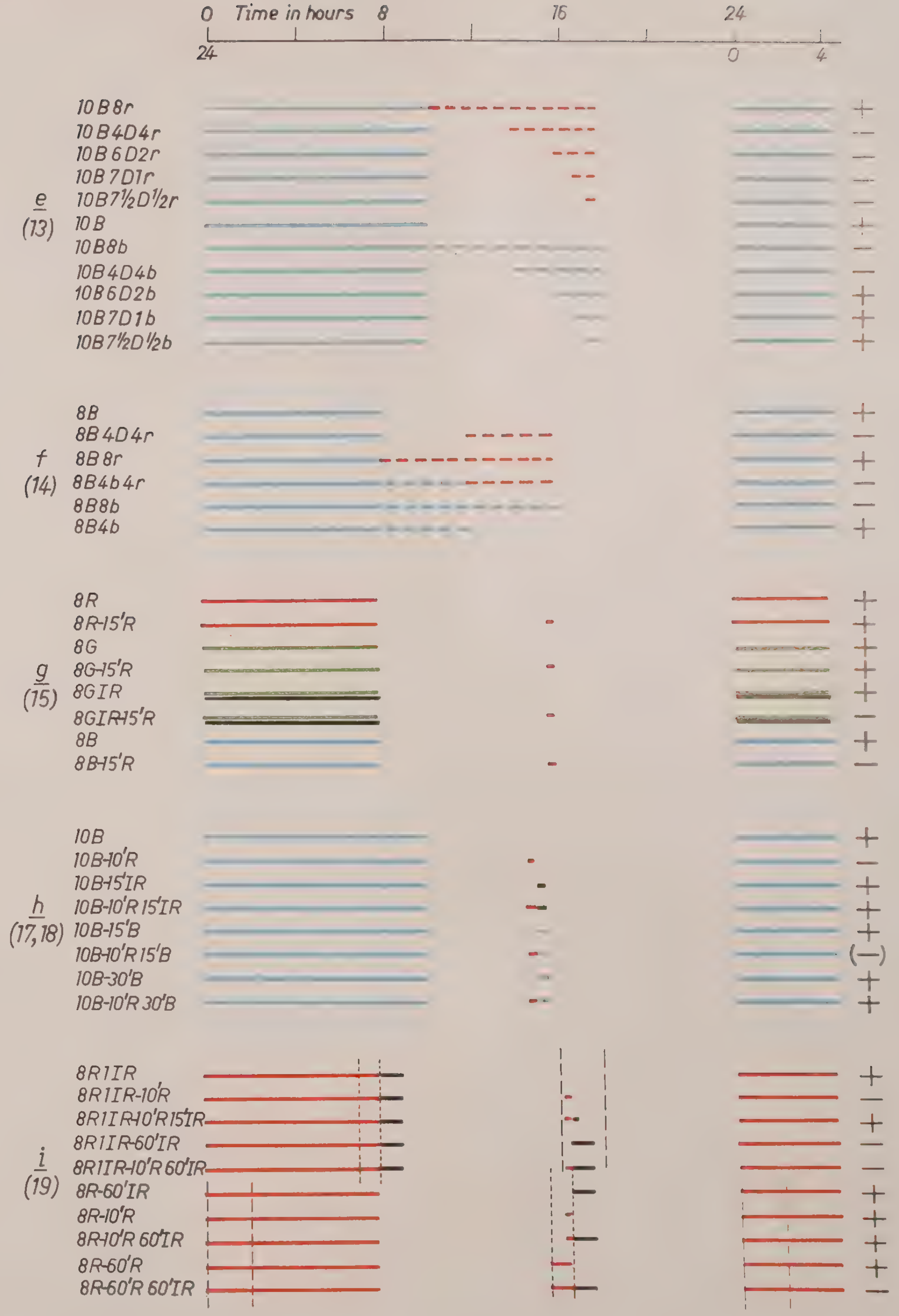

Plate 2

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THE BATRACHOSPERMETO-CHAETOPHORETUM, A REMARKABLE ALGAL ASSOCIATION IN THE NETHERLANDS

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(Goes)

(received March 12th, 1959)

In 1949 Westhoff called attention for the first time to the remarkable submerged algal growth of *Batrachospermum moniliforme* and *Chaetophora incrassata* on stalks of reed and *Typha*, observed in a fragment of the *Scirpeto–Phragmitetum* in Botshol, a small lake near the village of Abcoude.

> "De stengels van *Phragmites* en *Typha* onder water zijn een dankbare standplaats voor plantaardig "lasion" of wel aangroeisel in de vorm van interessante en vaak zeer fraaie blauw-, rood- en groenwieren, waarvan sommige wellicht min of meer kenmerkend voor associatie of verbond zullen blijken te zijn: ik noem *Batrachospermum* sp., een der weinige inlandse roodwieren, die niet in uitgesproken brak of zout water leven, het puimsteenachtige, met kalk geïncrusteerde groenwier *Chaetophora incrassata* fo. *crystallophora*, de blauwwieren *Rivularia dura*, *Phormidium laminosum*, *Schizothrix coriacea*, etc." [1])

I have studied this algal vegetation also in various ponds and pools, and I found it representing a rather constant association with probably a wide distribution: the *Batrachospermeto–Chaetophoretum*. It appeared, however, that this association is by no means a characteristic epiphytic community, for it also occurs on stones and live snails.

The nomenclature used for the algae follows Pascher, Süsswasserflora. Diatoms and desmids have not been studied.

Floristic composition

The *Batrachospermeto–Chaetophoretum* is highly characterized by the combination of *Batrachospermum moniliforme* and *Chaetophora incrassata*. The first species, however, is characteristic for the association only in the stagnant waters of ponds and lakes; in streams it occurs in a quite other vegetation and is then often allied with the moss *Platyhypnidium rusciforme* (Neck.) Fleisch. *(Oxyrrhynchietum rusciformis*, Gams, 1927; vide von Hübschmann, 1953). Israelsson (1942) considers it as a rather

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[1]) "The submerged stalks of *Phragmites* and *Typha* form a very suitable habitat for vegetable lasion in the form of interesting and often beautiful Cyanophyceae, Rhodophyceae and Chlorophyceae, some of which may be perhaps more or less characteristic for association *(Scirpeto Phragmitetum)* or alliance *(Phragmition):* I mention *Batrachospermum* sp., one of the few native red algae, which do not live in brackish or salt water, the pumiceous, lime-incrusted green alga *Chaetophora incrassata* fo. *crystallophora*, the bluegreen algae *Rivularia dura*, *Phormidium laminosum*, *Schizothrix coriacea* etc." (Transl. author).

TABLE I

BATRACHOSPERMETO–CHAETOPHORETUM

Number:	1	2	3	4	5	6	7	8	9
Covering in %:	10	30	5–10	60	65	40	40	40	5
Batrachospermum moniliforme	1	3	+	2	2	2.3	1	+	2
Chaetophora incrassata	1	+	2	2	3	2	2	3	2
Chaetonema irregulare	—	+	—	—	+	—	—	—	+
Cladophora glomerata	+	+	+	1	2	+	2	—	2
Oedogonium sp.	—	+	+	+	—	+	1	+	+
Spirogyra sp.	—	+	—	—	—	—	+	+	+
Mougeotia sp.	—	—	+	—	—	—	+	+	+
Tolypothrix lanata	—	—	—	+	1	—	—	2	1
Ophridium versatile	—	—	+/1	—	+	+	—	+	—
Draparnaldia plumosa	2	+	—	+	—	—	—	—	—
Rivularia biasolettiana	—	—	—	—	+	+	—	+	—
Euspongilla lacustris	+	+/1	+	—	—	—	—	—	—
Enteromorpha prolifera	+	—	—	1	—			—	—
Coleochaete scutata	—	—	—	+	—	—	+	—	—
Ophiocytium parvulum	—	—	—	+	—	—	—	+	—
Nostoc sphaericum	—	—	—	—	+	—	—	+	—
Schizochlamys gelatinosa	—	—	—	—	—	—	—	1	+
Bulbochaete sp.	—	—	—	—	—	—	—	+	+
Ophiocytium maius	—	—	—		—	—	—	+	+
Stigeoclonium tenue	—	+	—	—	—	—	—	—	—
Phormidium tenue	—	+	—	—	—		—	—	—
Cordylophora caspia	—	—	—	—	—	—	—	—	—
Hydra vulgaris attenuata	—	—	+	—	—	—	—	—	—
Phormidium tinctorium	—	—	—	+	—	—		—	—
Dichothrix baueriana	—	—	—	—	—			+	—
Chlorococcum wimmeri		—	—	—			—	+	—
Microcystis aeruginosa	—	—	—	—	—	—	—	—	+

LEGENDA:

1. Prov. of Utrecht; Botshol near Abcoude, ca. 15 km south of Amsterdam. Bruggesloot, on reedstalks along the bank, opposite to the farm of Mr. M. Verwey. Lasion of *Batrachospermum moniliforme*, *Chaetophora incrassata* and many specimens of *Draparnaldia plumosa*. Surface: 1 m²; depth 40 cm; Cl′-content 842 mg/l; 27-V-'56; CH 56016 A.
2. Botshol, in a small pool between the Bruggesloot and the Kleine Wije, and connected with these waters. Beautiful *Batrachospermum*-growth on the submerged parts of *Phragmites*- and *Typha*-stalks, but only on the mown stalks, not found on the juvenil shoots. Very sheltered station. Surface: 10 m²; depth 30–50 cm; Cl′-content in March 1956: 450 mg/l; 24-III-'57; CH 57004.
3. Botshol, in the south-western part of the Grote Wije on mown *Typha*-stalks and on *Potamogeton pectinatus;* bottom covered by *Chara hispida*. Epiphytic vegetation of *Chaetophora* and *Batrachospermum*. Surface: 5 m²; depth 80–100 cm; Cl′-content in March 1956: 479 mg/l; 24-III-'57; CH 57005.
4. Botshol, very sheltered small pool connected with the Vliet, ca. 100 m north of the large willow tree, with a community of *Nymphaea alba*, *Utricularia vulgaris* and *Phragmites*. On reedstalks a luxuriously developed *Batrachospermum–Chaetophora*-growth, in which brown clods of diatoms are covering 40–50 %. Surface: 1 m²; depth 50–80 cm; Cl′-content very variable, in March 1956: 392 mg/l, in June 1956: 1123 mg/l; 16-VI-'57; CH 57009.
5. Prov. of North Holland; Naardermeer, between the towns Weesp and Naarden, ca. 20 km east of Amsterdam; Side-ditch of the Hoofdtocht, west of the Machine-

tocht. Very fine *Chaetophora–Batrachospermum*-vegetation on reedstalks. Surface: 2 m²; depth 50 cm; 30-V-'54; CH 54044.

6. Naardermeer; in a ditch nearly closed by vegetation, parallel with the Hoofdtocht, between Spookgat and Grote Meer. Extremely sheltered station with beautifully developed *Hydrochareto–Stratiotetum*. On reedstalks a dense *Batrachospermum–Chaetophora*-vegetation. Surface: 2 m²; depth 45 cm; 2-VI-'57; CH 57007.
7. Prov. of Utrecht; Oud Loosdrecht, ca. 8 km west of Hilversum, along the bank of the Loenerveense Plas. Well-developed vegetation of *Chaetophora incrassata*, *Batrachospermum moniliforme* and *Cladophora glomerata*, on stones, heavily shaded by *Scirpus lacustris* and *Salix* sp. Surface: 1 m²; depth 20–30 cm; 10-VII-'55; CH 55035.
8. Prov. of North Holland; Petten, pool in the dune valley Rietput with dense vegetation of Characeae, *Potamogeton natans* and *P. gramineus*. On stalks of reed and *Carex lasiocarpa* a luxurious *Chaetophora incrassata*-lasion. Surface: 3 m²; depth 20–40 cm; 22-V-'54; CH 54029.
9. Prov. of South Holland; Island of Voorne, Quackjeswater. Fine *Chaetophora–Batrachospermum*-vegetation in a shaded station along the bank, on submerged branches, *Phragmites*- and *Typha*-stalks. Surface: 1 m²; depth 40–50 cm; 23-V-'54; CH 54030.

indifferent species, occuring in different kinds of water, not related to the amount of electrolytes. In the Netherlands, however, it shows a distinct preference for eutrophic and mesotrophic ponds; it is absent from waters poor in electrolytes.

Chaetophora incrassata has its optimum in this association but cannot be considered as an exclusive species, because it may be found also in the *Cladophoretum glomeratae lacustre*. In running water, however, it is very rare. The only specimens, collected in slowly flowing water, present in the Rijksherbarium, have been found by Sprée near Lochem (12-IV-1860). Luther (1953) who mapped the distribution of the species in Scandinavia, discovered a remarkable preference for areas rich in lime. *Chaetophora* occurs also occasionally in oligohalinous water¹), so the dependence from lime is not certain. It is clear, however, that the species needs a high concentration of electrolytes. The maximal salinity tolerated in nature was 2.1 ⁰/₀₀ Cl′, according to Waern (1952). These findings of Scandinavian investigators, hold also for the Dutch waters, where I found the association to be common in eutrophic and mesotrophic freshwater as well as in oligohalinous water with a salinity up to 1,3 ⁰/₀₀ Cl′. It tolerates pollution of the water very well, but it was not yet observed in industrial sewage. The hemisphaerical juvenil stages of the species often have been confounded with *Chaetophora elegans* and *Ch. pisiformis*.

Chaetonema irregulare is a minute epiphytic alga, occurring on *Chaetophora* as well as on *Batrachospermum* in the gelatinous layer around the stems; however, it is difficult to discover. Although it is presented only 3 times in the table, it nevertheless may be a species of common occurrence.

In addition to the characteristic species of the association the green alga *Cladophora glomerata* and the bluegreen alga *Tolypothrix lanata* are

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¹) The chlorinity of fresh water amounts to 0–0,3 ⁰/₀₀ Cl′. For oligohalinous and mesohalinous water these values respectively are 0,3–1,6 ⁰/₀₀ and 1,6–9 à 10 ⁰/₀₀ Cl′ (System of Välikangas–Remane).

often abundant. Contrary to *Batrachospermum*, *Cladophora glomerata* prefers the most illuminated spots in the association. It is very ubiquitous and dominates in very different vegetations, viz. in the *Cladophoretum glomeratae lacustre*, in the meso- to polyhalinous *Cladophoreto–Polysiphonietum* DEN HARTOG, n.p.), and) in the rheophilous *Cladophoreto–Lemaneetum (= Cladophoretum glomeratae rheobenthicum* SYMOENS, 1957). Even in the mountainous *Hydruretum foetidi* it sometimes may dominate.

Tolypothrix lanata, and more rarely *T. tenuis* and *T. distorta*, too, form beautiful coloured bushes on the reedstalks. Other companions of the association, rather inconspicuous, but nevertheless always present in more or less large quantities, are *Spirogyra* sp., *Mougeotia* sp. and *Oedogonium* sp. However, I found them always in a sterile state.

Further *Rivularia biasolettiana* (incl. *R. dura*) is a common species, occurring on reedstalks, wood, *Chara hispida*, *Potamogeton pectinatus* and stones. This species is also abundant in the *Cladophoretum glomeratae lacustre*. Also the large brightgreen colonies of the ciliate *Ophridium versatile* Ehrb. may be found on all imaginable substrates but they prefer hydrophytes as *Potamogeton* and *Chara* for attachment.

Coleochaete scutata occurs in small numbers on *Typha*- and *Phragmites*-stalks, but is much more abundant on the undersurface of the leaves of *Nymphaea alba*, *Nuphar luteum* and *Stratiotes aloides*.

More or less characteristic for eutrophiated waters are *Stigeoclonium tenue* and *Draparnaldia plumosa*. They have been found in the *Batrachospermeto–Chaetophoretum* along the banks of frequently used ditches between the meadows, in ponds and pools connected with them, and in the vicinity of farms. Last mentioned species tolerates very large fluctuations in salinity.

In oligohalinous waters *Enteromorpha prolifera* is often abundant in the association. This species, however, reaches its optimum in the meso- and polyhalinous *Enteromorphetum prolifero-intestinalis*, where it often is the dominant species (DEN HARTOG, n.p.). Diverse bluegreen algae occur frequently in the association. I collected *Dichothrix baueriana*, *Microcystis aeruginosa*, *Nostoc sphaericum*, *Oscillatoria amphibia*, *Phormidium laminosum*, *P. tenue*, *P. tinctorium* and *Schizothrix coriacea*. Probably this list can be enlarged.

In the samples of the *Batrachospermeto–Chaetophoretum* from the dunepools I found also *Schizochlamys gelatinosa*, *Bulbochaete* sp. and *Ophiocytium maius*. These species are reported to occur in the other lakes investigated, but were absent in the samples studied by me.

SYNECOLOGY

The association occurs in clear freshwater under eutrophic and mesotrophic conditions. In the oligohalinous water of Botshol it is exposed to considerable annual fluctuations in chlorinity. In spring chlorinity amounts to 0,3–0,5 $^0/_{00}$; in summer it increases to 1,1–1,3 $^0/_{00}$, decreasing again in autumn. In the other localities investigated chlorinity is low. In the eutrophic Naardermeer it amounts to 0,05–0,14 $^0/_{00}$, in the mesotrophic Loenerveense plas to 0,03–0,04 $^0/_{00}$, in the dunepools Quakjeswater and Rietput to 0,1 $^0/_{00}$.

The association mostly occurs on the submerged parts of old stalks and roots of *Phragmites*, frequently also on *Typha* stems, more rarely on *Equisetum fluviatile*, *Potamogeton pectinatus*, *P. compressus* and *Chara globularis*. In addition to the epiphytic occurrence epilithic and epizoic growth were also observed. I found beautiful examples of the association on shells of live *Limnaea stagnalis* (L.) and *Planorbis corneus* (L.), so the minimum area of the community is very small. As stones are dumped only in localities exposed to wave-action, where the *Batrachospermeto–Chaetophoretum* does not occur, the association is in our country mainly epiphytic.

The *Batrachospermeto–Chaetophoretum* occurs in rather shaded localities where too small quantities of light penetrate for the very photophilous *Cladophoretum glomeratae lacustre*. In the Loenerveense Plas near Oud Loosdrecht, where both communities occur together, I only found the *Batrachospermeto Chaetophoretum* on stones, heavily shaded by *Salix*-shrubs along the banks of the pond, the light from the other side being intercepted by dense facies of *Scirpus lacustris*.

In reedborders the sciaphilous habit of the association causes a very remarkable distribution on the algal vegetation. On the most exposed, outermost stalks of the reedborder the *Batrachospermeto–Chaetophoretum* is absent from 0–15 cm below the water level, and has been replaced

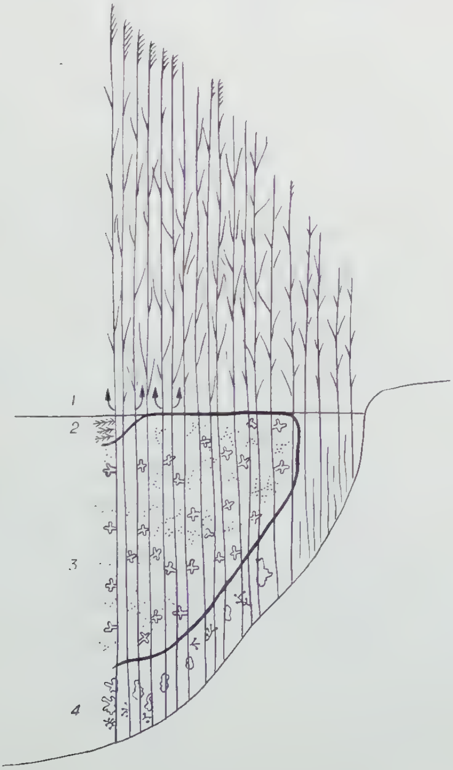

Fig. 1. Transsect of a reedborder. 1 = *Omphalia belliae*, 2 = *Cladophora glomerata*- facies, 3 = *Batrachospermeto–Chaetophoretum*, 4 = coenose of *Cordylophora caspia* and *Euspongilla lacustris*.

by *Cladophora glomerata*, rarely accompagnied by other algae in this habitat. In a depth below –15 cm the fragile *Batrachospermum* plants and the brightgreen bushes of *Chaetophora incrassata* appear.

In clear water they descend to 70–80 cm, rarely to 1 m depth in the outside of the reedborder. More inward in the reed-edge, where the quantity of light decreases, the upper limit of the association coincides with the water level, while the lower limit may be reached already at 30 cm depth. The lower limit of the association is often determined by competition with zoocoenoses, in which the hydroid *Cordylophora caspia* (Pall.), the mussel *Dreissena polymorpha* (Pall.) and the sponges *Euspongilla lacustris* (L.) and *Ephydatia fluviatilis* (L.) are leading forms. On the reedstalks in Naardermeer and Botshol a narrow belt of the fungus *Omphalia belliae* Johnst. may be found slightly above the water level in autumn. A scheme of the zonation in reedborders is given in Fig. 1.

Life cycle

The annual rhythm of the association has been studied from 1954 to 1957 in Botshol. Here *Chaetophora incrassata* appears a few weeks after disappearance of the last ice, thus generally speaking in March.

The species soon increases in numbers and it is common during spring and summer. In October and November it dies. Occasionally in winter some hemisphaerical, 1–2 mm large individuals may be found. *Batrachospermum moniliforme* occurs during the whole year, and probably may live several years. Immediately after melting of the ice gonimoblasts are formed, which may be found to halfway May. In summer and autumn gonimoblasts have been found only exceptionally. In May everywhere the germlings can be found; they grow out in the course of the year to very large, blackish or greenish bushes. The largest plants, found by me, measured up to 25 cm, but these plants were probably several years old individuals. In some localities in Botshol *Batrachospermum* disappears in summer owing to the continually rising chlorinity; the tolerance to high chlorinity of *Batrachospermum* is considerable lower than in the case of *Chaetophora*.

After cold winters an interesting zonation may be observed. In 1956, after the very cold February-month, I found in Botshol, immediately below the water level a 25 cm broad belt of *Chaetophora* germlings. With greater depth the numbers of *Chaetophora* decreased, but here enormous bushes of *Batrachospermum*, with welldeveloped gonimoblasts occurred. In the end of May this zonation-pattern had become indistinct by settling of young *Batrachospermum* in the uppermost belt. Nevertheless in the deeper water the *Batrachospermum*'s were considerably larger. The cause of this temporary zonation was the ice-layer, measuring 25 cm, and killing all algae by freezing. After melting of the ice *Chaetophora* could develop directly, by germinating of resting stages. The invasion of *Batrachospermum* followed somewhat later in the season, after development of the carpospores, formed in the gonimoblasts.

Classification of the association

Westhoff (1949) supposed the algal lasion of *Phragmites*- and *Typha*-stalks to contain characteristic species for the *Scirpeto–Phragmitetum* or

Phragmition. This supposion was based on the misconception, that a mutual affection occurs between *Scirpeto–Phragmitetum* and its submerged lasion. This is by no means the case. The algal vegetation in reed-borders develops only in such places, where light conditions and also exposition to wavedashing are favourable. It is, however, indifferent to the kind of substrate, which only serves for attachment. It is absent from thin reed- and *Typha* beds, which are exposed to wave-action. The combination of *Batrachospermeto–Chaetophoretum* and *Scirpeto-Phragmitetum*, although often found, has to be considered as an occasional one.

The *Batrachospermeto-Chaetophoretum* must be classified as a part of the freshwater-series of the *Cladophora*-formation, by reason of its physiognomy, its life-form pattern and its stratification.

SUCCESSION AND COMPETITION

Observations on succession and competition have been made in Botshol and Naardermeer from 1953 to 1957. The *Batrachospermeto–Chaetophoretum* only has been met with on reed- and *Typha* stalks more than a year old. On young stalks no algal vegetation occurs, owing to the rapid growth of the reed. On young shoots only species of *Hydra* have been found, in Botshol mainly *Hydra vulgaris* f. *attenuata* Pall., in other ponds *Pelmatohydra oligactis* Pall. may be the dominant species, while also other *Hydra*'s may occur. When the growth of the reed declines and comes to a stand-still, settlement of other species takes place. What species will establish themselves depends mainly on the quantities of light and on the exposure to wave-action. At the end of the summer and in autumn settlement of *Cordylophora caspia*, *Euspongilla lacustris* and a number of algae viz. *Nostoc sphaericum*, *Phormidium tenue*, *Oedogonium* sp., *Spirogyra* sp., and the small hemisphaerical form of *Chaetophora incrassata* may be observed. *Batrachospermum* settles rarely in the first year. In sheltered localities the algae are highly favoured by the scanty movement of the water. They crowd out nearly all animals, which are driven back to the deepest parts of the reedstalks. The limit between the *Batrachospermeto–Chaetophoretum* and the zoocoenose below it, is determined by mutual competition.

However, the animal colonies prefer stations more exposed to water-movement, and here the algae stand little chance of settling. Only *Cladophora glomerata* competes succesfully with the animals and occupies the belt of 0–15 (25) cm below the water level. The remaining parts of the stalks are densely covered by *Cordylophora caspia* and *Dreissena polymorpha*, on the deepest parts also by the sponges *Euspongilla lacustris* and *Ephydatia fluviatilis*. The inconspicuous *Hydra*-species remain common. In exposed stations in the lakes and ponds of Friesland and the north-western part of Overijsel the same zonation occurs, but here the Bryozoon *Plumatella fungosa* (Pall.) is often dominant.

Animals feeding on algae have been observed in very small quantities in the *Batrachospermeto-Chaetophoretum*. Their influence is negligible. Only the following snails were found: *Planorbis planorbis* (L.), *Acroloxus*

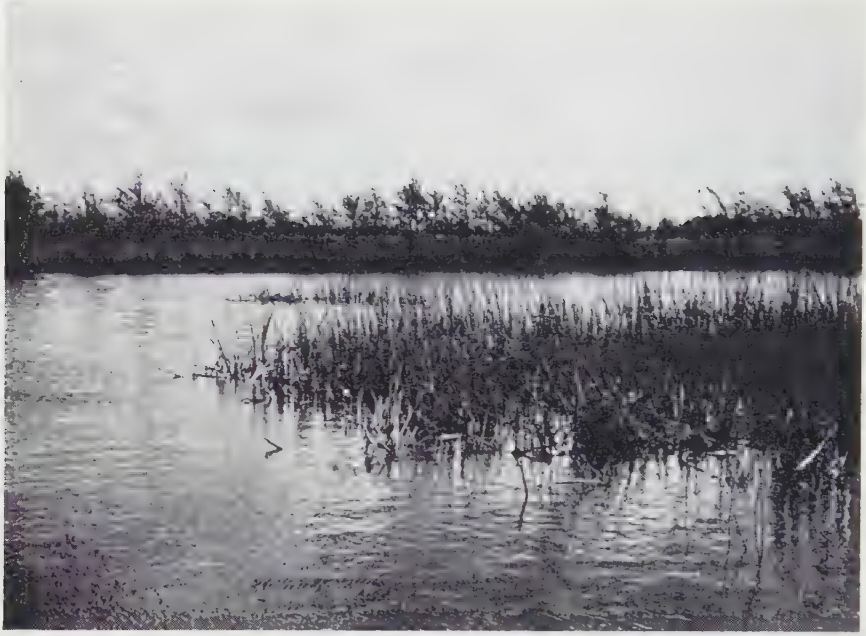

Fig. 2. Sheltered locality with *Phragmites*- and *Typha*-growth in the northern part of Botshol; a typical station of the *Batrachospermeto–Chaetophoretum*.

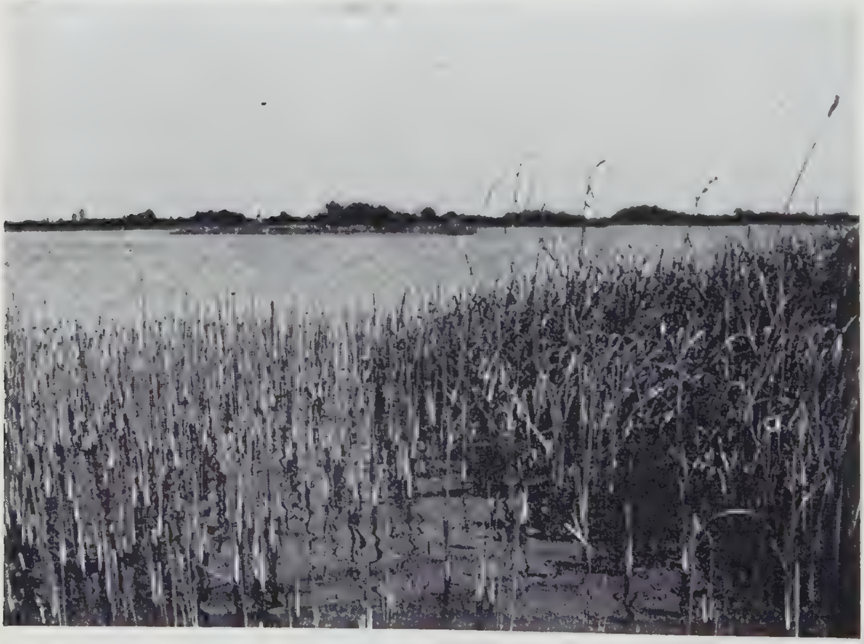

Fig. 3. Stand of *Typha latifolia*, exposed to wave-action along the Grote Wije, Botshol. The submerged lasion of this vegetation is characterized by the hydroid *Cordylophora caspia*. To the right *Cladium mariscus* is visible.

lacustris (L.), *Bythinia tentaculata* (L.), *Limnaea palustris* (Müll.) and *Theodoxus fluviatilis* (L.).

Other animals observed in this association are the leeches *Theromyzon tessulatum* (O. F. Müll.) and *Piscicola geometra* (L.). The first species is a parasite of waterbirds. In Botshol it is observed only rarely outside the *Batrachospermeto–Chaetophoretum*. In the Naardermeer, where extensive parts of the watersurface are covered by the leaves of *Nymphaea alba*, it is confined to them, and was never observed in the reedborders. *Piscicola geometra*, a parasite of fishes, occurs only in the outermost part of the reedborder, in sheltered as well as in exposed stations.

DISTRIBUTION

The association is widely distributed in the lakes and ponds of the western part of the Netherlands. I ascertained its occurrence in the Botshol, the Naardermeer, the broads of Loosdrecht (Loenerveense Plas, Eerste Loosdrechtse Plas), the broads of Nieuwkoop, ditches in the Alblasserwaard, near Kudelstaart and near Nigtevegt. No data are available from the lakes of the north-western part of the province of Overijsel. In the turbid lakes of the province of Friesland I did not succeed in finding the association but Mr. A. S. Tulp kindly send me a fine sample of *Batrachospermum moniliforme*, collected on reedstalks in the Groote Wielen near Leeuwarden.

Except in the lacustrine district the association occurs in dunepools (Rietput and Tweede Korfwatertje near Petten, Quakjeswater).

No doubt the *Batrachospermeto–Chaetophoretum* occurs in other parts of Europe. KROK (1869, cited by LUTHER, 1953) mentions *Chaetophora incrassata*, together with *Batrachospermum moniliforme* and *Draparnaldia glomerata* (= *D. plumosa)* from the Bothnian Gulf near Haparanda, where the salinity amounts to ca. 1 $^0/_{00}$ NaCl. MARGALEF (1953) found the association of *Batrachospermum moniliforme* and *Chaetophora incrassata* in a small, slowly running stream with *Potamogeton*, *Callitriche*, *Nasturtium* and a grass, in the north-eastern part of the Balearic island Majorca. Besides the characteristic species he found also *Draparnaldia plumosa*, *Spirogyra* sp., *Tolypothrix distorta*, much diatoms and a few desmids, which findings enlarge the agreement with the Dutch vegetation. However, the mass-occurrence of *Cladophora fracta rivularis* and the mosses *Platyhypnidium rusciforme* and *Fontinalis durieui* points to the *Oxyrrhynchietum rusciformis*, the moss-dominated association of eutrophic running water. Thus in slowly running water both associations can occur mixed.

Dr E. KANN kindly informed me, that she observed *Batrachospermum moniliforme* together with *Chaetophora cornu-damae* (= *Ch. incrassata)* in the Traunsee in Austria. Some vegetations described by WAERN (1939) from the Swedish lake Tåkern and by KANN (1958) from lakes in Holstein show a close floristic relation with the *Batrachospermeto–Chaetophoretum*, but are not identical.

SUMMARY

The *Batrachospermeto–Chaetophoretum* is a very characteristic algal association, widely distributed in oligohalinous as well as in eutrophic and mesotrophic freshwater in the lakes and ponds in the western part of the Netherlands. It prefers shaded stations, sheltered from wave-action and occurs on reeds, *Typha* stalks and waterplants, but also on stones and live snails. The association may be found the whole year round; *Batrachospermum moniliforme* is a perennial species, propagating in spring, *Chaetophora incrassata* an annual one. Owing to its small light requirement the association is bordered at the upper limit by the photophilous *Cladophoretum glomeratae lacustre;* the lower limit is determined by competition with sessile animal colonies. Probably the association has a wide distribution in Europe.

ACKNOWLEDGEMENTS

I am much indebted to Dr. J. Th. Koster (Leyden), who identified some Cyanophyceae from the samples, and to Dr. P. Bourrelly (Paris), Dr. T. Christensen (Copenhagen), Dr. E. Kann (Vienna), Dr. H. Luther (Helsinki) and Dr. R. Margalef (Barcelona) for personal communications on the distribution of the association. Further I wish to express my gratitude to the direction of the "Vereniging tot Behoud van Natuurmonumenten" for the permission to carry out my investigations in its domains, and to Mr. R. J. de Wit (Amsterdam) for assistence in obtaining permission to study the algal vegetation of Botshol in the breeding season. Dr. K. F. Vaas (Leyden) kindly corrected the English text.

REFERENCES

Hartog, C. den. 1958. Epilithische algengemeenschappen in Nederland. Handel. Hydrobiol. Ver. **10**: 6–8.

Hübschmann, A. von. 1953. Einige hygro- und hydrophile Moosgesellschaften Norddeutschlands. Mitt. Flor-soz. Arbeitsgem. **4**: 15–25.

Israelsson, G. 1942. The freshwater Florideae of Sweden. Symb. Bot. Upsal. **6,1**: 1–134.

Kann, E. 1958. Der Algenaufwuchs in der eulitoralen Zone alpiner und norddeutscher Seen. Verh. intern. Ver. Limnol. **13**: 311–319.

Krok, Th. O. B. N. 1869. Bidrag till kännedomen om Alg-floran i inre Östersjön och Bottniska viken. Öfvers. K. Vet.-akad. Förh. **26**: 67–92.

Luther, H. 1953. Über die Nordische Verbreitung von Chaetophora incrassata (Huds.) Hazen. Bot. Not.: 317–340.

Margalef, R. 1953. Materiales para la hidrobiologia de la isla de Mallorca. Publ. Inst. Biol. Aplic. **15**: 5–111.

Symoens, J. J. 1957. Les eaux douces de l'Ardenne et des regions voisines: Les milieux et leur végétation algale. Bull. Soc. Roy. Bot. Belg. **89**: 111–314.

Waern, M. 1939. Epilithische Algenvegetation, in G. E. du Rietz a.o. Zur Kenntnis der Vegetation des Sees Tåkern. Act. Phytogeogr. Suec. **12**: 43–50.

———, 1952. Rocky shore algae in the Öregrund Archipelago. Act. Phytogeogr. Suec. **30**: 1–298.

Westhoff, V. 1949. Landschap, Flora en Vegetatie van de Botshol nabij Abcoude. Baambrugge. 102 p.

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A NEW CARABIDICOLOUS SPECIES OF THE GENUS *LABOULBENIA* FROM SUMATRA

(ASCOMYCETES, LABOULBENIALES)

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(Zoölogisch Museum, Amsterdam)

(received March 10th, 1959)

In the course of investigations carried out in the Zoological Museum at Amsterdam, a considerable amount of material of Laboulbeniales was obtained from beetles of the family Carabidae from the Indo-Australian region. An extensive report on this collection is in preparation. In the present paper one of the most distinct species collected is described and I take pleasure in dedicating this species to Prof. Dr. J. Heimans in grateful recognition of his drawing my attention to this fascinating group of Fungi and his stimulating interest in the progress of my work.

Laboulbenia heimansii nov. spec.

Material. — 2 full-grown individuals taken from the inferior surface of the prothorax of a specimen of *Casnoidea interstitialis* Schm.–Goeb. from Sumatra: Manna, 1902, Coll. M. Knappert (slide nr. Z. M. A. 359).

Latin description. — Proxima *L. concinnae* Thaxt., sed forma longiore et graciliore differt. Receptaculum pallide lutescens, hyalinum, distaliter paullo dilatatum. Cellulae III et VI angustiores, quam in *L. concinna* pro rato longiores, cellula V cellulam III haud attinginte. Perithecium pro rato brevius et latius quam in *L. concinna*, paraphysibus minus numerosiores. In *Casnoidea interstitiali* occurit. Typus: Museum Zoologicum Amstelodamensium, prep. No. Z.M.A. 359.

Description. — Receptacle very pale yellowish, rather weakly punctulate distad of cell I. Cell I large, subcylindrical, the basal half gradually tapering towards the foot-cell. Cell II about half as long as cell I, but of about the same width, cylindrical, anterior and posterior sides of equal length, the proximal and distal septa marked by slight constrictions. Cells III and IV subequal, each about half as long as cell II. Septum between cells III and IV marked by a slight constriction. Cell VI somewhat longer than cell III, about two thirds of cell II. Cell V rather small, separated from cell IV by an oblique septum, therefore not in contact with cell III. Cell VII also rather small and only a little broader than cell V, bulging a little at the anterior side. Insertion-cell normally developed, almost horizontal, black. Basal cells of perithecium elongate so as to form a hyaline neck-like stalk for the perithecium. The curvature of this stalk causes the perithecium to bend away from the longitudinal axis at an angle of about 45°.

Perithecium opaque, brownish black, except at the somewhat translucent lip-cells. Perithecium rather long, rather slender (possibly due to shrinkage during the long time of dry preservation), broadest at about one third of its length, asymmetrically and gradually tapering towards the apex. Apex shortly cylindrical. Mouth of perithecium opening distally, with a wide slit on the lateral side.

Outer basal cell of appendages rather broad but short, a little prominent on the posterior side, its distal septum blackened, the branches broken off. Inner basal cell of about the same size as the outer, giving rise to a tuft of apparently rather short, unbranched paraphyses with blackened septa.

Total length to tip of perithecium: 385–440 μ; largest width: 45–50 μ; length to insertion-cell: 210-240 μ; perithecium exclusive of stalk: 135-160 μ × 48–50 μ; perithecium including stalk: 175–210 μ.

With the number of described species, subspecies and varieties coming near to 500, the genus *Laboulbenia* is the largest of its order. The last comprehensive treatment of the genus was given by THAXTER

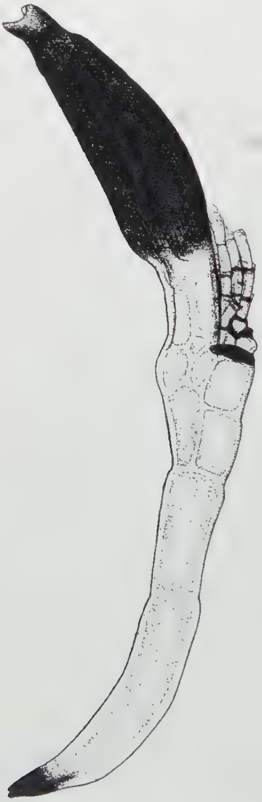

Fig. 1. *Laboulbenia heimansii* nov. spec., type specimen.

in the 2nd part of his unsurpassable monograph and dates from 1908. Since that time, however, many new species have been described, partly by THAXTER in his preliminary papers, partly by SPEGAZZINI and others. Obviously, a revision of *Laboulbenia* was planned by THAXTER, but unfortunately this revision never appeared owing to his untimely death in 1932.

In view of these circumstances, the description of a new species of *Laboulbenia* has become a somewhat hazardous undertaking nowadays.

To determine the relationship of the presently described species it seems fully justified to restrict the discussion to those forms occurring on Carabid hosts, since the species described from other Coleopterous families and insect orders other than Coleoptera apparently either belong to specific and rather disjunct groups or pertain to the complex of certain polyphagous species like *L. flagellata* Peyr., *L. polyphaga* Thaxt., etc.

Among the Carabidicolous species of *Laboulbenia* an entirely free and stalked perithecium such as in the presently described species is by no means a normal feature. The character is obviously one of a derivative nature, and the species in which it occurs are to be looked upon as highly differentiated. We find a stalked perithecium in a number of species parasitic on hosts belonging to quite disjunct tribus of the family Carabidae, like, for instance, the Panagaeini *(L. brachionychi* Thaxt., *L. brachionychi* subsp. *euschizomeri* Speg.), the Pterostichini *(L. orthomi* Thaxt., *L. cauliculata* Thaxt., *L. colpodis* Thaxt.), the Helluodini *(L. helluodis* Thaxt.), the Dryptini *(L. galeritae* Thaxt., *L. decipiens* Thaxt., etc.), etc. The morphological differences between the groups of parasites infesting these host categories show that, on the one hand the stalked perithecium was acquired along different phylogenetic lines and, on the other hand, a certain degree of host specificity of the species-groups of *Laboulbenia* with regard to the host categories exists.

It is, therefore, not surprising that the nearest relative of *L. heimansii*, *L. concinna* Thaxt. 1902 from "*Casnonia*" spec.[1]) from Buitenzorg, Java, came from a host species belonging to the same tribus as *Casnoidea interstitialis* Schm.-Goeb., viz. the Colliurini. *L. heimansii* and *L. concinna* agree largely in the conformation of the receptacle, the relation of the perithecium to the receptacle and the characters of the appendages. *L. concinna*, however, may be easily distinguished by the dark colour of the receptacle distad of cell I, the less elongate and more club-shaped receptacle, the comparatively broader cells III and VI, the relatively larger cell V, which is separated from cell IV by a vertical septum and thus is in contact with cell III, and the more copiously developed appendages.

As regards the relationship of *L. concinna*, THAXTER (1908) did not give an opinion, and the place the species was given, viz. between *L. rhinophora* Thaxt. and *L. imitans* Thaxt., does not appear to have much significance in this respect. Indeed, *L. concinna* and *L. heimansii* seem to stand rather isolated, in particular among the other species recorded from hosts of the tribus Colliurini.

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[1]) According to CSIKI (1927-1933) the name *Casnonia* is no longer in use. The Indonesian species previously referred to this genus apparently now belong to the genera *Colliuris* and *Casnoidea*.

According to my unpublished host-index of the Carabidicolous Laboulbeniales the following species of *Laboulbenia* have been recorded from the Colliurini, sensu Csiki (1927–1933).

Host genus	Parasite	Recorded also from hosts of the tribus	Geographical distribution
Colliuris	*L. casnoniae* Thaxt.	Pterostichini, Lebiini	Oriental, Australian Palearctic, Ethiopian and Neotropical regions
	L. equatorialis Thaxt.	—	Neotropical region
	L. falcata Thaxt.	—	Neotropical region
	L. flaccida Thaxt.	—	Neotropical region
Casnoidea	*L. casnoniae* Thaxt.	See above	
	L. heimansii nov. spec.	—	Oriental region
"Casnonia" (Casnoidea or *Colliuris)*	*L. asiatica* Thaxt.	—	Oriental region
	L. bottegoi Speg.	—	Ethiopian region
	L. concinna Thaxt.	—	Oriental region
Calophaena	*L. minima* Thaxt.	Lebiini, Agrini	Neotropical region
	L. triordinata Thaxt.	—	Neotropical region
Eudalia	*L. eudaliae* Thaxt.	—	Australian region
Leptotrachelus	*L. minima* Thaxt.	See above	
Pionycha	*L. minima* Thaxt.	See above	

Of these species, *L. casnoniae* doubtlessly belongs to the complex of *L. flagellata* Peyr. and apparently takes the place on the Colliurini and Lebiini of the latter which focusses on the Pterostichini. Only a single record of *L. casnoniae* from Pterostichini is known, but this may be considered somewhat doubtful since the locality of the particular host, *Homothes elegans* Newm., an Australian species, was given as "India".

L. flaccida, according to Thaxter (1908), is related to *L. planetis* Thaxt. from *Planetes* (Zuphiini) and *L. helluodis* Thaxt. from *Helluodes* (Helluodini), and was compared also with *L. casnoniae*. It seems to be a more differentiated form belonging to the complex of *L. flagellata*.

Possibly related to the species of the *flagellata*-complex, though decidedly more disjunct, is *L. asiatica*, which is closely related to *L. celestialis* Thaxt. from *Drypta* (Dryptini) and *Dicranoncus* (Pterostichini) and apparently also to *L. acrogenis* Thaxt. from *Acrogenys* (Zuphiini). By evidence of the characters of the appendages, in particular the inflated outer basal cell, *L. equatorialis* and *L. falcata*, two somewhat isolated species, seem to show affinity to *L. asiatica*.

L. eudaliae was compared with *L. loxandri* Thaxt. from *Loxandrus* (Pterostichini) by Thaxter, but the relationship was considered quite uncertain. The characters of the appendages, however, seem to show some similarity with those of *L. equatorialis* and *L. falcata:* the inflated outer basal cell characteristic for the latter two species and *L. asiatica* is also typically developed in *L. eudaliae*.

Together with *L. casnoniae*, *L. minima* so far is the only species parasitic on Colliurini which has been recorded from other Carabid tribus, but probably Thaxter united several species under this name. *L. minima* was compared with *L. longicollis* Thaxt. from *Galerita* (Dryptini) by Thaxter in 1908 in spite of the totally different conformation of the receptacle. *L. longicollis*, a species with a stalked perithecium, superficially somewhat resembles *L. heimansii*, but differs in particular by the structure of the appendages. In that respect it differs also from *L. minima* and the relationship between *L. longicollis* and *L. minima*, therefore, seems rather remote. On the other hand the appendages in *L. minima* are not unlike those in *L. concinna* and *L. heimansii*, and *L. minima*, although strongly differing in habit, may be regarded as the nearest relative of *L. concinna* and *L. heimansii*. On the whole, these three species appear related, though not particularly closely, to the group of *L. asiatica*, *L. equatorialis*, *L. falcata* and *L. eudaliae*.

L. triordinata among the other species occurring on Colliurini stands quite isolated. It is decidedly related to *L. helluomorphae* Thaxt. from *Helluomorpha* (Helluonini) and *Pleuracanthus* (Helluonini) and *L. perplexa* Thaxt. from *Galerita* (Dryptini), as stated by Thaxter, as well as to other species described from *Galerita*.

L. bottegoi, finally, was described without reference to other species. It seems to be a minute and rather insignificant form pertaining to the complex of *L. polyphaga* Thaxt., a species with a wide host-distribution focussing on Harpalini.

Summarizing the above discussion we may say, that the species of *Laboulbenia* parasitic on hosts of the tribus Colliurini do not form a cohesive group but rather fall apart in several more or less unrelated categories. Of these the group embracing *L. minima*, *L. heimansii* and *L. concinna*, apparently having no definite relatives on other Carabid tribus, seems to be the most characteristic. The species of the other groups have their nearest relatives on Pterostichini, Harpalini, Lebiini, Agrini, Dryptini, Zuphiini, Helluodini, and Helluonini.

It may be of interest, especially to Coleopterologists, to pass some remarks here on the information which the systematic relationship of the parasites may supply on the affinities of their host-group to other Carabid tribus. Although it is quite clear that there exists no absolute parallel in the taxonomy of insects and the Laboulbeniales which infest them, there can be no doubt that the host-distribution of the species of *Laboulbenia* is not a random one, and that, in general, it gives some indication as to the interrelationship of the hosts.

In the present case, there is no doubt that the Colliurini through their parasites show a strong affinity to the tribus Lebiini, Agrini, Dryptini, Zuphiini, Helluodini and Helluonini. These six groups, together with some others, partly raised to the rank of families, have been recently united in a superfamily Lebiomorphi by Jeannel (1949), and were opposed, amongst the superfamilies Harpalomorphi, Callistomorphi and Masoreomorphi, to the Odacanthomorphi, a superfamily largely agreeing in concept with the tribus Colliurini sensu Csiki.

In view of the evidence supplied by the relationships of the species of *Laboulbenia* occurring on Colliurini, however, it may be remarked tentatively, that the distinctive characters of this tribus as against the six other tribus may have been somewhat overestimated by Jeannel.

The indications towards a relationship of the Colliurini with the Pterostichini and Harpalini also may be of importance. The fact, however, that these indications are given mainly by two weakly differentiated species, *L. casnoniae* and *L. bottegoi*, reduces somewhat their significance.

ACKNOWLEDGEMENTS

I wish to express my indebtedness to Dr. G. Kruseman, Amsterdam, who has greatly facilitated my work on Laboulbeniales at the Zoological Museum, and to Dr. M. A. Donk, Leiden, and Dr. P. Vermeulen, Amsterdam, for advisory remarks. The aid of Dr. H. Sleumer, Leiden, with the translation of the latin diagnosis is also appreciated.

REFERENCES

An extensive bibliography of the Carabidicolous Laboulbeniales will be given in my forthcoming paper. In connection with the present paper the following references are the most important.

Csiki, E. 1927–1933. Carabidae in Junk & Schenkling, Cat. Coleopt. **1–3**.
Jeannel, R. 1949. Adephaga in Grassé, Traité de Zool. **9**: 1027.
Spegazzini, C. 1915. An. Mus. Nac. Hist. Nat. Buenos Aires **26**: 451.
Thaxter, R. 1895. Mem. Amer. Acad. Arts Sci. **12**: 187.
——— 1908. Mem. Amer. Acad. Arts Sci. **13**: 217.

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FLORAE MALESIANAE PRECURSORES XXII
CLADIUM AND MACHAERINA (Cyper.)

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(received March 10th, 1959)

The circumscription of the genus *Cladium* as adopted by Bentham (1883), Pax (1887), Clarke (1908), and also recently by Kükenthal (1942), in his monographic treatment, has often been criticized and with good reason, for it covers species so heterogeneous that they can not be considered congeneric.

Cladium was published as a monotypic genus based on *C. jamaicense* Crantz from the West Indies (Browne, 1756; Crantz, 1766). After Brown (1810) had extended it considerably by the inclusion of a number of Australian species, several authors of the last century restricted it again to the immediate allies of *C. jamaicense*. For the other species some new genera were created, such as *Machaerina* Vahl (1806), *Baumea* and *Vincentia* Gaudich. (1829), *Chapelliera* Nees (1834), which were reduced once more to sections or subgenera of *Cladium* by Bentham and his followers. This reduction, however, was neither accepted by Palla (1902), who on morphological and anatomical grounds reinstated *Baumea* as a separate genus, nor by Stapf (1914), who transferred a number of Malaysian *Cladia* to *Vincentia*, with the remark that the West Indian *Machaerina* approaches so closely to *Vincentia* that its claim to generic rank might be questioned.

Lately Koyama (1956) divided *Cladium sensu lato* into two genera, one comprising *C. jamaicense* and its immediate allies only, the other embracing those species formerly referred to *Machaerina*, *Baumea*, *Vincentia*, or *Chapelliera*. I fully agree with him that this procedure results in two well-circumscribed, natural groups of generic rank, and that the correct names respectively are *Cladium* and *Machaerina*.

To the numerous characteristic features of both genera as tabulated by Koyama (1956, p. 60), I might add some often overlooked or undervalued differences. Bentham ascribed to *Cladium* in its wide sense "glumae undique imbricatae", Pax "Deckschuppen spiralig oder nur sehr undeutlich 2-zeilig", and Clarke (1894) "glumes imbricate on all sides". Kükenthal (1944) divided the subfamily *Rhynchosporoideae* into three tribes: *Schoeneae* with 3 stigmas and distichous glumes, *Cladieae* also with 3 stigmas but the glumes spirally arranged, and *Rhynchosporeae* with 2 stigmas. It is somewhat surprising that in this very simplified system *Remirea maritima* Aubl. and *Actinoschoenus thouarsii* Kunth, both with exactly distichous glumes, are placed in *Cladieae*. As to *Cladium sensu stricto*, the glumes are here certainly spiral, but in *Machaerina* in Koyama's sense I always find the arrangement to be distichous, as was already stated by excellent observers such as Kunth and Nees. The best characterization of the spikelet is perhaps that given by NEES (1846–47) for his genus *Chapelliera:*

"Dispositio squamarum et bracteolarum spiculae in universum haec est: Spiculis ternis bracteolae sunt duae, squamis latiores, spiculis lateralibus a latere incumbentes. Squamae sunt distichae: inferior paulo minor et sterilis; secunda fertilis ♀; tertia isti aequalis, sterilis; quarta minor, flore hermaphrodito saepe abortivo; quinta inclusa exigua."

When KÜKENTHAL (1942, p. 164) says that *Cladium distichum* C. B. Clarke stands apart in the genus (as circumscribed by him) because of the exactly distichous arrangement of the glumes, I can not agree with him. The two-ranked disposition of the glumes is much accentuated in the proliferous spikelets of *Cladium distichum*, but can also readily be observed in those *Machaerina* species with several-flowered spikelets, such as *M. articulata* (R. Br.) Koyama, *M. aspericaulis* (Kük.) Koyama, *M. iridifolia* (Bory) Koyama, etc. It must, however, be borne in mind that the bract and the prophyll of the lateral spikelets (one of them or both may be present) are placed transversally with respect to the glumes. Very rarely I found the uppermost, sterile glume also placed transversally, *e.g.* in *Machaerina gunnii* (Hook. f.) Kern. This irregularity may be caused by the ripening fruit pushing aside the tiny glume.

KÜKENTHAL (1942, p. 2) drew attention to another important character peculiar to *Cladium sensu stricto* but lacking in *Machaerina*, *viz* the saucer-shaped disc below the nut, not unlike that frequently found in *Scleria*. In *Cladium mariscus* (L.) Pohl, from which in my opinion *C. jamaicense*, *C. procerum* S. T. Blake, etc. are only racially distinct, this disc usually remains on the rhachilla when the fruit falls off. Though less conspicuous than in *C. mariscus*, a disc is also found in the North-American *C. mariscoides* (Muehlenb.) Torr. The incrassate, obpyramidate stipe of the nut in some species of *Baumea*, according to KÜKENTHAL (1942, pp. 2 & 6) a rudimentary disc, is morphologically quite different.

The hollow stems of *Cladium* in contrast to the pithy or septate ones of *Machaerina* may possibly also furnish a distinctive generic character.

There are some regrettable inaccuracies in Koyama's extensive list of transfers to *Machaerina*.

It is generally accepted that *Cladium vauthiera* Clarke and *C. borneense* Clarke belong in *Lepidosperma*, *Chaetospora capillacea* Hook. f. in *Tetraria*, *Cladium cyperoides* Merr. in *Fimbristylis*, *Cladium melleri* Baker and *C. pantapodum* Baker in *Costularia*, *Cladium monocarpum* Black and *Schoenus punctatus* R. Br. in *Schoenus*, and *Cladium procerum* S. T. Blake is a true *Cladium*. Their transfer to *Machaerina* obscures the delimitation of this genus, and disagrees with the principle that the useless creation of new names should be avoided.

The authority cited in parentheses is not always correct: the basionym of *Machaerina iridifolia* is *Scirpus iridifolius* Bory, *Machaerina laxa* should be based on *Chapelliera laxa* Nees, *Machaerina scirpoidea* on

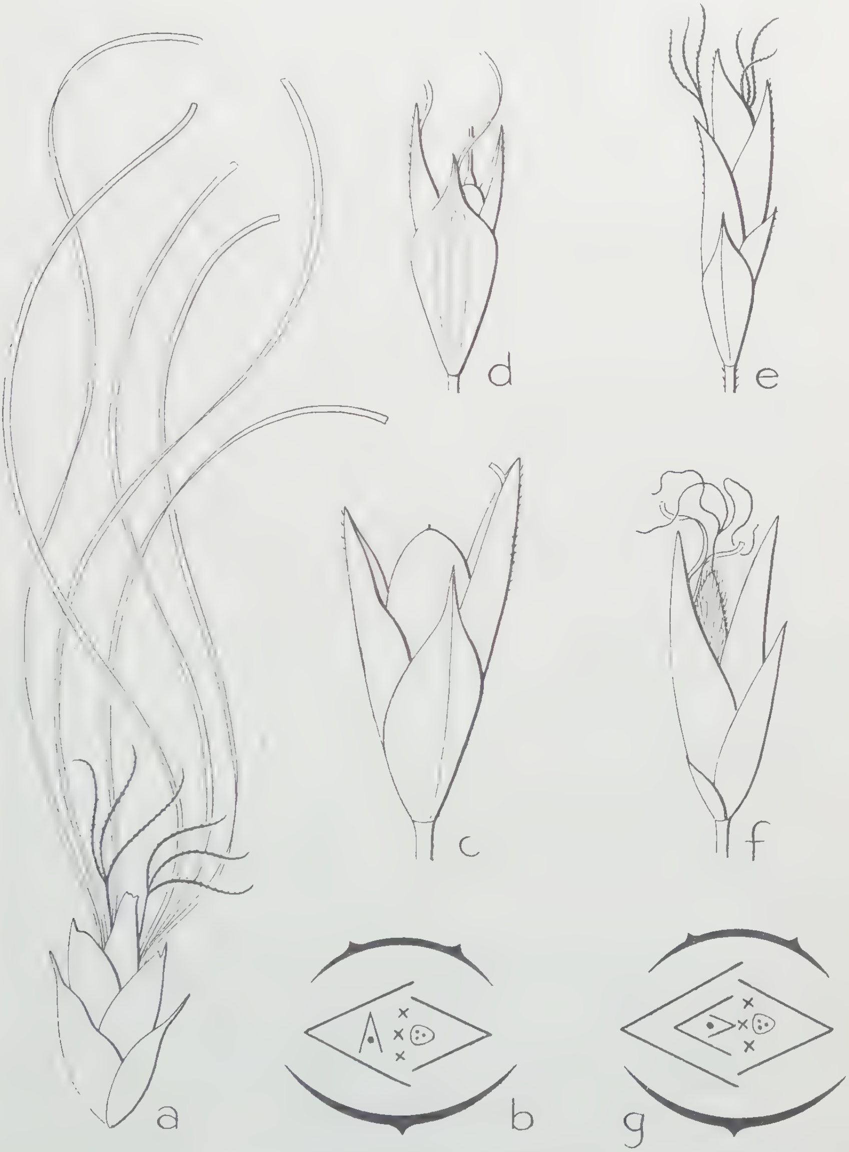

Fig. 1. *a:* spikelet of *Machaerina sinclairii* (Hook. f.) Koyama; *b:* diagram of lateral spikelet of *M. gunnii* (Hook. f.) Kern; *c:* spikelet of this sp.; *d:* spikelet of *M. deplanchei* (Boeck.) Koyama; *e:* spikelet of *M. articulata* (R. Br.) Koyama; *f:* spikelet of *M. mariscoides* (Gaudich.) Kern; *g:* diagram of 1-flowered lateral spikelet of *Machaerina* sp. — All spikelets × 7.

Terobera scirpoidea Steud., and *Machaerina tetragona* on *Lepidosperma tetragonum* Labill.

While arranging the *Machaerina* collections of the Leyden Herbarium, it appeared necessary to make the following new combinations:

Machaerina acuta (Labill.) Kern, comb.nov.—*Schoenus acutus* Labill., Nov. Holl. Pl. Sp. 1:18, t. 18. 1805.

Machaerina flexuosa (Boeck.) Kern, comb. nov.—*Scirpus iridifolius* Poir. in Lamk, Enc. Méth. Bot. 6:783. 1806, non Bory (1804).—*Baumea flexuosa* Boeck., Abh. Nat. Ver. Bremen 7:39. 1880.

Machaerina gunnii (Hook. f.) Kern, comb. nov.—*Cladium gunnii* Hook. f., Fl. Tasm. 2:95. 1858.—See S. T. Blake (1943).

Machaerina lamii (Kük.) Kern, comb. nov.—*Cladium lamii* Kük., Bull. Jard. Bot. Btzg III, 16:309. 1940.

Machaerina mariscoides (Gaudich.) Kern, comb. nov.—*Baumea mariscoides* Gaudich. in Freyc., Voy. Bot.: 417. 1829.—*Cladium gaudichaudii* W. F. Wight, Contr. U. S. Nat. Herb. 9:230. 1905.—*Machaerina gaudichaudii* (W. F. Wight) Koyama, Bot. Mag. Tokyo 69:64. 1956.

In 1905 the epithet *mariscoides* was not transferable to *Cladium* because of the already existing combination *Cladium mariscoides* (Muehlenb.) Torr. In *Machaerina* the earliest epithet *mariscoides* has to be used.

Machaerina nuda (Steud.) Kern, comb. nov.—*Schoenus nudus* Steud., Syn. 2:165. 1855.

In several cases I can not agree with Koyama as to the systematic value of taxa originally described as species. As to the Malaysian *Machaerinae*, *M. disticha*, *M. philippinensis*, and *M. micranthes* are in my opinion not specifically distinct, and so are *M. arfakense* and *M. teretifolia*, *M. crinita* and *M. sinclairii*, *M. sinuata* and *M. glomerata*, *M. iris* and *M. falcata*.

Koyama also transferred *Cladium undulatum* Thwaites to *Machaerina*, but in my opinion this species is neither a *Cladium* nor a *Machaerina*. Kükenthal placed it in *Cladium sect. Obtusangula* next to *Cladium philippinense*, *C. distichum*, and *C. articulatum*, which, however, are certainly not its nearest allies. Its leaves are dorsiventrally flattened and spirally disposed in a basal rosette. Clarke and others described the spikelets as being 1–2-flowered with the lower flower perfect, but in the numerous spikelets I examined I always found a single flower only without a small sterile glume above it (see Clarke 1909). The nut, hairy at the top, with thin exocarp and 3 longitudinal pale ribs is quite different from the thick-walled hard nut in *Machaerina*. Perianth-bristles are not found in *Cladium*. In *Machaerina* they rarely occur (*e.g.* in *M. restioides* and *M. maingayi*), and here they are always very delicate and capillary. The bristles in *Cladium undulatum*, however, are whitish, flattened and scale-like, very similar to those of *Lepidosperma*, but hairy and not thickened after anthesis. The species occurs also in Australia. Bentham (1878) placed it in *Tricostularia*, as *T. fimbristyloides* F. v. M., and remarked that it is very nearly allied to *Cladium undulatum* from Ceylon and to an "unpublished Borneo species", which three might almost rank as a distinct genus. The Ceylon and Borneo plants are undoubtedly conspecific with the Australian ones and their systematic place is rather in *Tricostularia* than in *Cladium* or *Machaerina*.

Tricostularia undulata (Thwaites) Kern, comb. nov.—*Cladium undulatum* Thwaites, En. Pl. Zeyl.: 353. 1864.

Here it may be remarked that nuts and bristles of the same type are found in *Chaetospora paludosa* R. Br., which Bentham also placed in *Tricostularia*. Kükenthal referred it to *Schoenus sect. Helothrix*, but it is very remote from the other species of this section, and the characteristic features of *Schoenus* — upper flower(s) reduced and upper internodes of the rhachilla elongated and zigzag — are not found in it. KÜKENTHAL (1938, p. 5) says that in *Tricostularia* the glumes are spirally arranged and the stamens inserted on a disc, but both objections to placing in *Tricostularia* are unsound.

As was already stated by KÜKENTHAL (1942, p. 193; 1952, p. 495) *Cladium stradbrokense* Domin is synonymous with *Trachystylis foliosa* S. T. Blake. This species has certainly nothing to do either with *Cladium*, or with *Machaerina*, and its transference to *Machaerina* seems unjustified. Because of its 1–2–flowered spikelets with several empty glumes at the base, Blake placed his genus *Trachystylis* in the tribe *Rhynchosporeae* next to *Actinoschoenus* and *Arthrostylis*, from which genera it was distinguished by the well-developed leaves, the umbel-like inflorescence, the bifid hispid style, and the 2 stamens. Blake admitted that in many characters *Trachystylis* is not unlike *Fimbristylis* of the *Scirpeae*, but apart from the tribal characters he thought the characters of style and nut rather different. The tribe *Rhynchosporeae* — even raised to the rank of a subfamily by several authors — is inadequately defined by few-flowered spikelets with several empty glumes at the base. Such spikelets are frequently found in *Scirpeae*, whereas on the other hand several-flowered spikelets are to be found in numerous species of *Schoenus*, *Machaerina*, and *Rhynchospora*. In *Scirpeae* the number of empty glumes usually varies from 0 to 2, but there are many exceptions, also in *Fimbristylis*. For instance, in the widely distributed *Fimbristylis monostachyos* (L.) Hassk. frequently the 4 lower glumes are sterile, the 3rd and 4th being of the same shape and size as the flower-bearing glumes. On the contrary several "rhynchosporoid" species have only 2 empty glumes at the base of the spikelet. The floral characters of *Cladium stradbrokense* are those of *Fimbristylis*, the leaves with their thickened margins and cellulose-reticulate upper side are characteristic of this genus, as is the anthelate structure of the inflorescence. In my opinion the species should be placed in *Fimbristylis*.

Fimbristylis stradbrokensis (Domin) Kern, comb. nov.—*Cladium stradbrokense* Domin, Bibl. Bot. Heft 85:476. 1915.—*Trachystylis foliosa* S. T. Blake, Proc. R. Soc. Queensl. 48:89. 1937.—*Trachystylis stradbrokensis* (Domin) Kük., Bot. Jahrb. 75:496. 1952—*Machaerina stradbrokensis* (Domin) Koyama, Bot. Mag. Tokyo 69:65. 1956.

REFERENCES

BENTHAM, G. 1878. Flora Australiensis **7**: 384.
————, 1883. In B. & H., Gen. Pl. **3**: 1065 1066.
BLAKE, S. T. 1943. Trans. R. Soc. S. Austr. **67**: 59.
BROWN, R. 1810. Prodromus Florae Novae Hollandiae: 236–238.
BROWNE, P. 1756. Civil and Natural History of Jamaica: 114.
CLARKE, C. B. 1894. In Hook., Fl. Br. Ind. **6**: 673.
————, 1908. Kew Bull., add. ser. **8**: 124–125.
————, 1909. Illustrations of Cyperaceae: t. 8, f. 9.
CRANTZ, H. J. N. VON. 1766. Inst. **1**: 362.
GAUDICHAUD, C. 1829. In Freyc., Voy. Bot.: 416–417.
KOYAMA, T. 1956. Bot. Mag. Tokyo **69**: 59–67.
KÜKENTHAL, G. 1942. In Fedde, Rep. **51**: 1–17; 139–193.
————, 1944. In Fedde, Rep. **53**: 218.
————, 1952. In Bot. Jahrb. **75**: 493–497.
NEES VON ESENBECK, C. G. 1834. Linnaea **9**: 298.
————, 1846–'47. In Lehmann, Pl. Preiss. **2**: 76, in nota.
PALLA, E. 1902. Allg. Bot. Zeitschr. **8**: 69.
PAX, F. 1887. In E. & P., Pfl. Fam. **2**^{2}: 116.
STAPF, O. 1914. J. Linn. Soc., Bot. **42**: 178–179.
VAHL, M. 1806. En. Pl. **2**: 238.

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BALLOTA NIGRA L. AUX PAYS-BAS

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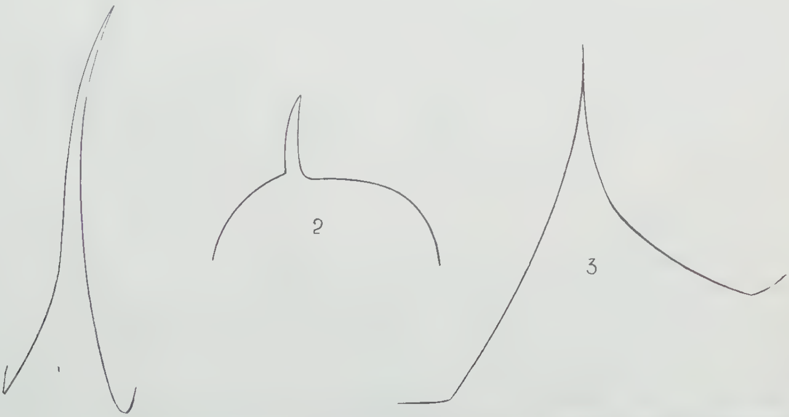
(reçu le 10 mars, 1959)

M. Patzak, dans son excellente étude "Revision der Gattung *Ballota* Section *Ballota*" (Ann. nathist. Mus. Wien, 62: 57–86, 1958) n'a guère cité des exemplaires des Pays Bas. Commes a carte de distribution indique que les deux sous-espèces de l'Europe centrale, *Ballota nigra* L. ssp. *nigra* et *B. nigra* L. ssp. *foetida* Hayek, ont été récoltées dans notre pays, il nous sembla utile d'étudier les spécimens qui se trouvent dans nos herbiers.

Presque tous les exemplaires néerlandais appartiennent au *Ballota nigra* ssp. *foetida*. En étudiant les nombreuses récoltes dans la collection du Rijksherbarium de Leiden, nous étions surpris de constater la grande diversité dans les formes des dents des calices de la ssp. *foetida*.

La forme des dents de la sous-espèce *nigra* est longue et étroite (Fig. 1); celle de la sous-espèce *foetida*, au contraire, est plus large (Fig. 2 et 3). Par conséquent le calice de la ssp. *nigra* est étroit, tandis que celui de la ssp. *foetida* est en forme de cloche.

Nous avons pensé à la possibilité que les plantes néerlandaises et celles d'Allemagne pourraient représenter une cline entre les exemplaires avec des dents selon la fig. 2 et la ssp. *nigra*. Dans ce cas il faudrait trouver une variabilité réduite dans le sud-ouest de l'Europe, mais il nous semble qu'une telle réduction n'existe pas.



Dents des calices de *Ballota nigra*, dessinés à la camera lucida. Fig. 1, ssp. *nigra* de Berlicum; Fig. 2, ssp. *foetida* de 's-Gravenhage, de Witte Brug; Fig. 3, ssp. *foetida* de 's-Gravenhage, Scheveningsche Boschjes.

Il existe probablement en Europe centrale une région où les deux sous-espèces *nigra* et *foetida* hybridisent.

Dans le Rijksherbarium de Leiden, il y a deux exemplaires (Leiden, buiten de Rijnsburgerpoort, 1856 et Nijmegen, Runmolenweg, 1934) qui forment probablement des intermédiaires entre les sous-espèces *nigra* et *foetida*.

Dans les Pays-Bas les localités de la ssp. *nigra* sont les suivantes:

Rijksherbarium, Leiden:

Deventer	Meelfabriek	1916	Kloos
,,	Meelfabriek	1919	Kloos
,,	Noury & v. d. Lande	1938	Holthuis
,,	Noury & v. d. Lande	1939	Jeswiet & Kloos
Zutphen	Langs een dijk	1919	Jansen & Wachter
Arnhem	Malburgsche-veer	1927	v. Soest
Nijmegen	St. Annalaan	1902	Kempers
,,	Voorm. Koornmolen St. Anna	1926	Kern & Reichgelt
Molen bij Mill		1926	leg. J. Kern
Berlicum	N. Br. pakhuis	1930	Kern & Reichgelt
Roermond	Heg	1906	Des Tombe
Wormerveer	Meelfabriek	1914	Kloos
Den Haag	Witte Brug	1913	v. Burkom
Middelburg	Meelfabriek	1916	Evers

Herbarium, Utrecht:

Laren (Geld.)		1916	Kooper

De cette liste il paraît que la majorité des plantes a été récoltée près de moulins ou d'usines, ou bien à des endroits qui sont bien connus par leurs plantes adventives. Il faut en conclure que pour les Pays-Bas la ssp. *nigra* ne sera jamais autre chose qu'une plante introduite.

Quant à la ssp. *foetida* les récoltes sont tellement nombreuses qu'il est impossible de les énumérer.

Alors nous arrivons aux conclusions suivantes: Les Pays-Bas forment une partie de l'aire de la ssp. *foetida*. Il faut admettre que les exemplaires néerlandais de la ssp. *nigra* ne sont que des plantes introduites.

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TYPIFICATION AND CONSERVATION OF GENERIC NAMES IN MUSCI

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The type method, incorporated in the International Code of Botanical Nomenclature (abbreviated ICBN) in 1930, has not yet been applied to a number of genera in the group *Musci*. In some cases the application published is not in accordance with the present Code. Of course the older authors did not use the type method explicitly. However, from their treatments typifications of older generic names can be derived in many cases. During the preparations for the Index Muscorum the history of many names had to be traced. The results, when needing comment, are discussed below.

Conservation, according to the ICBN, may be proposed "in order to avoid disadvantageous changes in the nomenclature" and should "preferably concern such names as have come into general use in the fifty years following their publication, or which have been used in monographs and important floristic works up to the year 1890" (art. 14). Conservation can be a necessary correction on changes in the Code. When the starting point for the nomenclature of *Musci* was changed from Linnaeus 1753 to Hedwig 1801 the priority of a number of names was altered. Necessary conservations have been proposed by Little, Bryologist 46: 105–125. 1940, accepted in due course with some exceptions. A clear example is *Barbula* Hedw., originally published by Hedwig in 1782, invalidated by the change of the starting point and in 1801 a later homonym of *Barbula* Loureiro 1790 in Phanerogamae. This has been corrected by conservation. The case of *Pottia* falls in this group.

Other names used in modern bryology without exception are nevertheless illegitimate because an older, neglected name has priority. Conservation may be considered in these cases. Perhaps there are more such names than traced up to now in the preparations for the Index Muscorum.

Typification can make a conservation necessary or highly desirable. The choice of the original author is decisive. If one element is present this is automatically the type. This is simple enough; nevertheless a peculiar problem arises when a single species mentioned in the publication of a new genus with a description afterwards appears to be based on a type specimen not fulfilling this description. The article accepted in the Amsterdam Congress (with the example of *Pseudotsuga mertensiana*) definitely fixes the meaning of the species concerned: it follows its type-specimen of the original publication.

As the genus follows the type-species, the meaning of the generic name is altered notwithstanding a clear description. It is irrelevant that probably the proposers of the article concerned did not foresee this consequence, nor that they possibly would not have had it included. Conservation of the name in a sense excluding the original type and selecting another type solves the problem. Perhaps some other wording of the ICBN would cover the problem. This, however, might have still other unforeseen consequences and conservation in special cases is to be preferred.

The case of *Conocephalum* Wiggers, on which I shook hands with Dr. Proskauer in the Paris Congress was partially related to this problem. Later Dr. Proskauer brought more facts to light and I can approve his new proposal. The case of *Macrohymenium* C. Muell. discussed below is a clear example.

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Acanthocladium. Established bryological custom treats this name in the sense used by Brotherus (1908 p. 1075). This excludes the two species from which the type ought to have been selected. The original publication of the name in *Musci* by Mitten, Trans. Proc. R. Soc. Victoria **19**: 86. 1882 was valid by a reference to the illegitimate homonym *Acanthodium* Mitten, Journ. Linn. Soc. Bot. London **110**: 182. 1868 non Delile 1812. Therefore, the type-species ought to have been selected from *Acanthodium papillatum* Mitt. or *A. rigidum* Mitt. Brotherus included the last species in *Trismegistia* C. Muell. and the first species was afterwards made the type species of the new genus *Acanthorrynchium* Fleisch. (Fleischer 1923, p. 1206). For the bryological established custom conversation in the sense of Brotherus is indicated, with *Acanthocladium extenuatum* (Brid.) Broth. as the lectotype, taking into account the publication of the section *Eu-Acanthocladium* Fleisch. (Fleischer, 1923, p. 1331). Conservation will affect *Acanthocladium* F. v. Mueller, Fragm. Phytogr. Austr. 2: 155. 1860–61, based on *A. dockeri* F. v. Mueller and given as a synonym of *Helichrysum* Vaill. in the Index Kewensis. The evaluation of a rejection of this name in the family *Compositae* can only be judged by phanerogamists and is not discussed here.

Acrocryphaea. This name was firstly published in Bruch, Schimper and Gümbel, 1850, Bryologia Europaea **5**: 35. (fasc. 44–45 Monogr. "*Cryphaea*" 2) as an invalid undescribed name. Three species were listed, including a new combination based on the Brasilian *Grimmia julacea* Hornschuch 1840 and an undescribed species *Acrocryphaea javanica* from Java. The next publication traced concerns Bryologia Javanica 2: 106. 1867, where van den Bosch and Lacoste definitely accepted *Acrocryphaea* "Hook., Bruch et Schimp." as a separate genus.

A generic description was not provided; nevertheless it is advocated that they validated the name by an indirect reference to the description of *Schoenobryum* Doz. et Molk., Musci Frondosi Inediti Archipelagi Indici 1848. 183. The Code does not define the indirectness of a reference, but the examples state it should be perfectly unambiguous. This criterion is certainly fulfilled here by listing *Schoenobryum* as a synonym of the species *Acrocryphaea concavifolia* (Griff.) Bosch et Lac. If his view be unacceptable, the validation will date from Brotherus (1905, p. 178). The name nevertheless is illegitimate at the same time for the same reason, the reference to an earlier valid synonym. The type of *Schoenobryum* Doz. et Molk. was certainly included in *Acrocryphaea* by v. d. Bosch and Lacoste, whether this be the Brasilian basionym of *Schoenobryum julaceum* (Hornsch.) Doz. et Molk., or the Javan specimens figured and certainly used by Dozy et Molkenboer in describing *Schoenobryum*. V. d. Bosch and Lacoste had no purpose of making a generic distinction between the Brasilian and Asiatic specimens and only used the genus in the same sense as had been done in the Bryologia Europaea. The treatment of v.d. Bosch and Lacoste has been followed by all authors treating *Acrocryphaea* as a genus separate from *Cryphaea* Mohr. Conservation is indicated in this case, as no single acceptance of *Schoenobryum* has been found during the preparations for the Index Muscorum. It will avoid the creation of about 30 new combinations.

Aerobryidium Fleisch. in Brotherus (1906, p. 820). The close cooperation of Fleischer and Brotherus permits the use of "in" here, for which definite proof is not known to the author. The formal choice of a lectotype has not been traced. Nevertheless it is clear from the original publication and Fleischer's treatment in 1923 that the species were grouped around the species with the oldest basionym: *Aerobryidium filamentosum* (Hook.) Fleisch.; therefore, this species is proposed here as the lectotype.

Aerobryopsis Fleisch. 1905, Hedwigia **44**: 304. The formal choice of a lectotype has not been traced. From the original species included in this genus by Fleischer three only remain as independent species now: *A. capensis* (C. Muell.) Fleisch., *A. longissima* (Doz. et Molk.) Fleisch. and *A. vitiana* (Sull.) Fleisch. From these ones *A. longissima* (Doz. et Molk.) Fleisch. was extensively studied by Fleischer and the only one figured. Therefore this species is formally proposed here as the lectotype.

Amblystegiella Loesk. 1903, Moosfl. Harz. 295. *A. sprucei* (Bruch) Loesk. was chosen as the lectotype by GROUT, 1932, Moss Fl. N. America 3: 142. The same species was named *Platydictya sprucei* (Bruch) Berkeley, 1863, Handb. Brit. Moss. 145 validly. The generic name *Amblystegiella*, therefore, is illegitimate. With a few exceptions all later authors treating the group as a separate genus used *Amblystegiella*. The exceptions did not concern *Platydictya* Berkeley, but the earlier subgenus *Serpo-Leskea*, raised to generic rank by LOESKE, 1905, Verh. Bot. Ver. Brandenburg **46**: 190. ('1904') erroneously counting priority from publication in another rank. No adoption of *Platydictya* Berkeley had been traced. Since the name *Amblystegiella* has been in use from 1903, compared with *Platydictya* Berkeley, conservation is proposed with kind permission of Prof. Dr. P. W. Richards (Bangor, Great Britain) who originally suggested the proposal.

Anacalypta Roehling ex Leman, 1816, Dict. Sc. Nat. 2, Suppl. 38. This name, revalidated earlier than *Pottia*, is based on a different type species. The present established custom is definitely uniting *Anacalypta* and *Pottia* taxonomically. Conservation of *Pottia* is necessary to correct this undesirable result of reversed priority by the change of the starting-point. See the discussion under *Pottia*.

Apodanthus La Pyl., Journ. de Bot. (Desvaux) 4(2):0.73.1814. This genus contained one species, *Apodanthus aphyllus* La Pyl., l.c. t. 33 f. 1, found among Splachnum. The figure given suggests some fungus; the dimensions are too small for any *Splachnum* or *Buxbaumia* species; *Ephemerum* species are out of question too for the absence of leaves. Perhaps an Ascomycete resembling *Cyathicula coronata* (Bull.) De Not. was concerned, but it is certainly not a moss in my opinion. If indeed belonging to fungi, the name will be invalid in this group, being published before the starting-point. The genus should be excluded from the *Bryophyta*.

Astomum Hamp. 1837, Flora **20**: 285. To fix the historical usage of this generic name *Astomum crispum* (Hedw.) Hamp. is proposed as the lectotype. However, Hampe's circumscription must be discussed. He included *A. alternifolium* (Hedw.) Hamp. in the genus, based on *Phascum alternifolium* Hedw. 1801. As pointed out under *Pleuridium*, this was the main element of Bridel's genus at the original publication and afterwards appeared to be based on specimens belonging to *Archidium* Brid. *Pleuridium* is proposed for conservation from a later date (1848). Acceptance of this proposal will remove any doubt on the legitimacy of the name *Astomum* Hamp.

Calyptrochaeta Desvaux, 1825, Mem. Soc. Linn. Paris 3: 226. This name is valid by the reference to the illegitimate name *Chaetephora* Brid., 1819 Mant. Musc. 148. (spelled *Chaetophora* on pag. XVII), *non* Schrank, 1789, Baierische Fl. **1**: 197. (Algae). Therefore, the type is automatically *Calyptrochaeta cristata* (Hedw.) Desvaux. This results in the genus being homotypic with *Eriopus* Brid., Bryol. Univ. 2: 788. 1827. In this page of the index of Bridel's last work the name is treated as an independent genus, with a reference to a subdivision *Eriopus* of *Chaetephora* Brid. on p. 339. This subdivision, however, is illegitimate as the type species of the genus is included. *Eriopus* is universally accepted and *Calyptrochaeta* is completely neglected. Conservation of *Eriopus* Brid. is proposed to legalise this custom for a characteristic genus of tropical mosses and to avoid more than 30 possible new combinations.

Dolichotheca Lindb., 1874, Notis. Sällsk. Faun. Fl. Fenn. 13: 417. is a genus of *Plagiotheciaceae* based on *D. repens* Lindb. with the basionym *Hypnum repens* Poll. 1777, now invalid as pre-Hedwigian and validated by Lam. et De Cand., 1805, Fl. Franç. **2**: 537. From the useful Index Nominum Genericorum I learned an earlier homonym published by

D. CASSINI, Dict. Sc. Nat. **51**: 476. 1827 (*Compositae*). The group of mosses concerned is rather small; taxonomically a number of bryologists do not recognise a separate genus, treating the species either as belonging to *Plagiothecium* or to *Isopterygium* Brid. Therefore, strong argument for conservation is lacking. Agreeing with Dr. J. J. Barkman (Wijster, Dr., Netherlands) in placing the European species in *Isopterygium*, I am obliged to use the combination *Isopterygium seligeri* (Brid.) Dix. in C. Jens., based on *Leskea seligeri* Brid. 1801, Musc. Rec. 2 (2):47, necessitated by the new opinion on the arbitrarily fixed date of HEDWIG, Species Muscorum 1801, altered from 31 Dec. 1801 to an earlier date.

Eriopus. Brid. The proposed conservation is discussed under *Calyptrochaeta* Desvaux.

Lamprophyllum. This name has been published for two different genera of Musci, both illegitimate because an earlier homonym exists: *Lamprophyllum* Miers, 1854, Proc. Linn. Soc. **2**: 338. (Guttiferae). *Lamprophyllum* Lindb., 1871, Act. Soc. Sc. Fenn. 10: 75 falls within the modern concept of *Pohlia* Hedw. 1801 and can be discarded. *Lamprophyllum* Schimp. 1856, Coroll. was published for *Hookeria splendidissima* Mont. 1835, Ann. Sc. Nat. Bot. ser. 2, 4: 97 without valid description. The name was validated by BROTHERUS (1907, p. 964). **Schimperobryum** Marg. **nom. nov.** is proposed here for this genus in *Hookeriaceae*. The typonym is *Lamprophyllum* Schimp. *ex* Broth., *in* Engl. et Prantl, Nat. Pflanzenfam. **1** (3): 964. 1907. The type species is *Schimperobryum splendidissimum* (Mont.) Marg. *nom. nov.*, based on *Hookeria splendidissima* Mont., Ann. Sc. Nat. Bot. ser. **2, 4**: 97. 1835.

Macrohymenium C. Muell. This name is proposed for conservation as an unfortunate consequence of the "*Pseudotsuga mertensiana* rule". The name was published validly by C. MUELL., 1847, Bot. Zeit. 5: 325. 1847 with only one species recognized, *Macrohymenium rufum* (Reinw. et Hornsch.) C. Muell. This species, therefore, automatically is the type species. It is immaterial in this respect that *Leskea acidodon* Mont. 1845 was included as a synonym.

Fleischer transferred the basionym of this type species to another genus of the same family *Sematophyllaceae* after studying "Originale" in the Berlin Herbarium. This transfer, *Acroporium rufum* (Reinw. et Hornsch.) Fleisch. (1923, p. 1672), though not treated by Fleischer as affecting *Acroporium* Mitt., 1868, Journ. Linn. Soc. Bot. London **10**: 182, does threaten the nomenclatural standing of this name. Nevertheless, this is not in line with the descriptions of C. Mueller and Fleischer of Macrohymenium, nor with established custom. This undesirable possibility should be discarded by the conservation of *Macrohymenium* C. Muell. *in* Doz. et Molk., 1848, Musci Frond. Inediti Archip. Indici **6**: 165. where the combination *Macrohymenium acidodon* (Mont.) Doz. et Molk. is published, which can be proposed as the lectotype of the name proposed for conservation.

Pleuridium. The name of this genus has been published by BRIDEL, 1819, Mant. Musc. 10. Two species were included: *P. alternifolium* (Hedw.) Brid., based on *Phascum alternifolium* Hedw. 1801, and

P. globiferum Brid. The type of the first species, the specimens found described and figured by DICKSON, Crypt. Brit. fasc. 1: 1 (t. 1 f 2) 1785 have been considered an *Archidium* species or equivalent to it by all British autors as far as I am aware and explicitly by MITTEN, publishing the combination *Archidium alternifolium* (Hedw.) Mitt. 1851, Ann. Mag. Nat. Hist. ser. **2,** 3: 30. followed by SCHIMPER in 1860. It has been suggested by BRUCH, 1825, Flora 8: 281 that the second species from Réunion is an *Archidium* too, but proof of this is unknown to me as is another identification. From Bridel's habitat notes it may be concluded that specimens were scarce. The type material most probably is destroyed. The genus has been emended by RABENHORST by including *Pleuridium subulatum* (Hedw.) Rabenh., Deutschl. Krypt. Fl. **2** (3): 79. 1848, based on *Phascum subulatum* Hedw. 1801, since continuously treated as an species of *Pleuridium*. The name from this author is proposed for conservation, chosing the *Pleuridium subulatum* as a lectotype for this purpose. This proposal has the advantage of unambiguously fixing the established custom of three generic names in Musci: *Astomum* Hamp., *Archidium* Brid. and *Pleuridium* Brid.

Pottia Ehrh. is invalidated by the change of the starting point for Musci from 1753 to 1801. The name was accepted afterwards by FUERNROHR, 1829, Flora **12** (**2**) Ergänzungsbl. p. 10. *Pottia truncata* (Hedw.) Nees et Hornsch. was selected as the type-species by WAREHAM *in* Grout, 1939, Moss Fl. N. America **1**: 197. The genus is universally accepted in this sence. Nevertheless the earlier validation of *Anacalypta* Roehl. ex Leman 1816 has priority since the change of the starting point when the two species are united as is the established custom now. Therefore *Pottia* Fuernr. is proposed for conservation.

SUMMARY

The argumentation is given for the conservation of the generic names in Musci: *Acanthocladium* Broth., *Acrocryphaea* B.S.G., *Amblystegiella* Loesk., *Eriopus* Brid., *Macrohymenium* C. Muell., *Pleuridium* Rabenh., *Pottia* Fuernr. The new generic name in *Hookeriaceae: Schimperobryum* Marg. is proposed, based on *Lamprophyllum* Schimp. ex Broth. A new specific combination is proposed: *Schimperobryum splendidissimum* (Mont.) Marg., based on *Hookeria splendidissima* Mont. 1835.

REFERENCES

BROTHERUS, V. F. 1906–1908. Musci *in* Engl. et Prantl, Die Natürl. Pflanzenfam. **1(3)**.

FLEISCHER, M. 1923. Musci Fl. Buitenzorg.

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PLANTSOCIOLOGICAL ANALYSIS OF MONTANE RAINFOREST NEAR TJIBODAS, WEST JAVA

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Introduction

The forest reserve on the twin volcanoes Mt Gede and Mt Pangerango, West Java, above the botanical garden Tjibodas, ranging from 1400–2900 m and comprising 1200 hectares, is a classical spot of botanical investigations. During more than a century these mountains have been visited by botanists, visitors as well as members of the staff of the Botanical Gardens at Bogor. Reinwardt, Blume, Korthals, Junghuhn, Zollinger and Teysmann made here investigations on the flora of Java during the first half of the nineteenth century. A more intensive study of the flora and the biology of plants and animals of this nature reserve started during the time of Treub, who opened in 1891 a guest house and a laboratory.

The forest between Tjibodas and the waterfalls of Tjibeureum was declared to be a nature reserve (see Docters van Leeuwen 1929). This was extended in 1926 to its present boundaries up to the summits of Gede and Pangerango which were especially studied by Docters van Leeuwen (1933). The reserve should be an entirely untouched forest where no felling of trees should be allowed.

F. W. Went (1945) called this forest a naturalist's paradise, "one of the best protected, best known and richest mountain forests of the tropics", and he wrote further about it: "A biologist's first impression is bewilderment. The forest seems a complete chaos. It takes a rather long and intimate association with a particular forest before the biologist starts to see some order in the arrangement of trees, shrubs, herbs, and epiphytes: then more general rules begin to emerge".

Tjibodas is thus an ideal place for ecological studies. For a botanical bibliography about Tjibodas see Van Steenis and Van Steenis-Kruseman (1953).

Method of work

The present author paid during his stay at Bogor 1952–1954 many visits to the biological station and nature reserve of Tjibodas with the aim to get such an intimate knowledge of the flora of this nature reserve that plantsociological studies could be started.

New collections for the local herbarium, which was destroyed during the war, could be made with the help of the very able plantcollectors Noerta, Hassan and Atting. Koorders' Flora of Tjibodas with some unpublished additions by Van Steenis (in the library of Herb. Bogoriense) and Backer's Beknopte Flora van Java (emergency edition) made it rather easy to name all collections to the species, and training in the field enabled me to recognize many trees from characters of bark and wood.

A new checklist of the flora (unpublished, copies in Herb. Bogoriense and archives of Flora Malesiana) showed the richness of this flora, comprising more than 900 species of phanerogams of which about 870 species are definitely native.

A method of a quadrate survey of one hectare as described by Richards (1952) was used during the first half of 1955 on Mt Sago near Pajakumbuh, W. Sumatra in a montane forest between 1000–1200 m altitude. During August of that year it appeared useful to compare this montane forest which was perhaps not quite undisturbed with analogous but untouched forest in West Java. No better place than the Tjibodas forest could be chosen for that.

In companion with Mr M. Jacobs and the mantris Noerta and Hassan we selected a sample plot, a quadrate of one hectare between the forest pathes "Djalan Batu gonggang" and "Djalan Pasarian" at some minutes walking from the mountain garden, at about 1450–1500 m altitude, a flat almost horizontal homogenous part of forest situated between two ravines. Only a part of the plot along the western margin is gently sloping, but influence of this could only be noted in the composition of the groundlayers of herbs where we noticed some species which seemed to be absent in other parts of the quadrate. The sample plot is almost undisturbed by human influence. Only in the south-east corner a gap occurs, about 15 × 30 m wide where a big tree had been blown down in a storm and after sawing had been carried out of the forest. The lower vegetation in this gap will be described separately. The corners of the quadrate are permanently indicated with iron plates.

The whole investigation of one hectare took six days. First we made a quantitative survey of the tree flora noting the name and diameter class of every tree with diameter above 10 cm after making a slash into the bark. The sample plot was investigated walking in four stretches and with each stretch a new list was made. After that we investigated in two corners of the sample quadrate two samples of 10 by 10 m in order to analyze the shrub layers, the herb layer and the trees under 10 cm diameter.

Finally the whole quadrate was searched for other species of herbs, shrubs, and young trees. Epiphytes were left out of consideration because they were already investigated by Went (1940). The number of their species may be estimated at about 100 (phanerogams and ferns). By collecting from Went's data those referring to epiphytes on tree species growing in this part of forest we get a detailed picture of the epiphytic flora. The results of our survey are represented in tables I to XI.

Discussion of the results

With this survey at hand we may discuss several aspects of the sociology of this type of forest. In the first place we may focus our attention to the total richness with species. Do we get with such a

Table I

The distribution of trees in the diameter classes:

diam. class no diam.	II 10-20 cm	III 21-30	IV 31-40	V 41-50	VI 51-60	VII 61-70	VIII 71-80	IX 81
number of trees . . .	121	44	39	21	16	20	20	3

Table II

Local aggregates of trees

List	1	2	3	4	total
Total trees numbered:	61	47	100	80	288
Villebrunnea rubescens	3	3	27	—	
Saurauia pendula	6	2	17	5	
Antidesma tetrandrum	—	1	—	8	
Viburnum sambucinum	—	—	—	4	
Macropanax dispersum	2	1	—	8	
Ehretia javanica	—	2	2	—	

Table III

The tree number/tree species relation (see also Fig. 1).

List	1	2	3	4	total
Total trees numbered in each list . .	61	47	100	80	288
Number of species in first list. . . .	29				29
Number of species added with		14			43
further listing			6		49
				10	59

survey a representative picture of this kind of forest? Which part of the total inventory of the montane forest at this height of the mountain is represented in this survey? Then we may try to get a picture of the structure, the complexity of the forest and the regeneration.

Total inventory of species

The area under investigation contains totally about 333 species of phanerogams and ferns. Among these are 78 species of trees, 40 species of shrubs, 30 of climbers, 10 of creepers, about 100 of epiphytes, and 73 of soil herbs, that is one third of the whole flora of the nature reserve which, according to our records, amounts to about 870 phanerogams and about 150 ferns and fern allies. Only 59 species of trees reach a diameter of 10 cm or more at breastheight. Thirteen species of trees able to reach diameters greater than 10 cm were only found as young trees, while six species never reach a diameter of 10 cm (Table V).

Some of these, like species of *Dysoxylum*, are more frequent in parts of the forest at lower altitude on the mountain. *Dysoxylum* rarely occurs higher than 1500 m altitude. *Podocarpus imbricata* does not play a great role in the forest near the garden, this tree being more numerous higher up the mountain. Species which "escaped" our survey and which occur in the same type of forest are nine in number: *Acronodia*

TABLE IV

Number of trees in the diameter classes

class	II	III	total
diameter cm	10-20	21-30	
Saurauia reinwardtiana	2		2
Eugenia laxiflora	2		2
Itea maxeophylla	3		3
Elaeocarpus pierrei	1		1
Tarenna spec.	2		2
Antidesma tetrandum	9		9
Laportea stimulans	3		3
Cestrum aurantiacum	1		1
Viburnum lutescens	1		1
Polyosma cf. integerrimum	1		1
Wendlandia glabrata	2		2
Acer niveum	2		2
Villebrunnea rubescens	32	1	33
Glochidion cyrtostylum	2	3	5
Acronychia laurifolia		1	1
Ficus ribes	7	2	9
Symplocos costata	1	2	3
Flacourtia rukam	1	1	2
Neolitsea cassiaefolia		1	1
Pygeum latifolium		1	1
Saurauia bracteosa		1	1
,, blumeana		1	1
Eurya cf. glabra		2	2
Turpinia pomifera	2	1	3
Viburnum sambucinum	4	1	5
Lindera polyantha		1	1

TABEL IV *(continuation)*

Number of trees in the diameter classes

class	II	III	IV	V	total
diameter	cm 10-20	21-30	31-40	41-50	
Saurauia pendula	23	6	1		30
Eugenia densiflora			2		2
,, clavimyrtus			1		1
Symplocos fasciculata	1		1		2
Phoebe spec.			1		1
Casearia coriacea			1		1
Ficus alba		2	1		3
Neonauclea obtusa			1		1
Ostodes paniculata	5	5		1	11
Vernonia arborea	1	1	1	1	4
Macropanax dispersum	8	—	2	1	11
Litsea mappacea			1		1
Mischocarpus frutescens			2		2
Quercus (coll. 28)			1		1
Litsea resinosa				1	1
Helicia javanica				1	1
Eugenia operculata		1	1	1	3

TABLE IV *(continuation)*
Number of trees in the diameter classes

class	II	III	IV	V	VI	VII	VIII	IX	total
diameter cm	10-20	21-30	31-40	41-50	51-60	61-70	71-80	81-130	
Pygeum parvifolium . . .					1				1
Eugenia tenuicuspis . . .		1			1				2
Quercus teysmanniana . .						1			1
Ficus variegata	1			1		1			3
Quercus pseudomolucca. .			3	2	1	1			7
Castanea argentea		5	6	4	5	4	1		25
,, javanica		1	1	1	—	1	2	1	7
,, tunggurut . . .			1	1			1	3	6
Quercus induta	1					1		1	3
Ilex pleiobrachiata							1		1
Manglietia glauca							1		1
Ehretia javanica						3		1	4
Machilus rimosa	2	1	3	3	1		1		11
Schima wallichii			1	2	1	3	1	3	11
Altingia excelsa	1	2	7	1	5	5	2	3	26
Engelhardtia spicata . . .								1	1
	121	44	39	21	15	20	10	13	283

punctata, *Litsea angulata*, *Litsea mappacea*, *Litsea noronhae*, *Glochidion macrocarpon*, *Neolitsea javanica*, *Sloanea zigun*, *Toona sureni* and *Ficus involucrata*. The three last mentioned species are rare at 1500 m as they reach their upper limit about this altitude. This makes a total list of about 87 species of trees in the forest between 1400 and 1500 m altitude. The bulk of this flora is thus represented within a sample plot of one hectare. The sample may serve as a qualitative one, fairly representative for the forest at this altitude (fig. 1 and Table III). If we take into consideration that KOORDERS' flora of 1914 contained 165 species of trees (among 575 phanerogams) and the total number of trees represented in our checklist of Tjibodas is about 172 (among about 870 of native not introduced phanerogams) we may assume that about half of the tree flora of the Mount Gede is represented in our survey.

Along the road to Air Panas (2000 m) the forest changes gradually in composition. *Schima* becomes more abundant. *Altingia* disappears at about 1700 m. Several species occur above 2000 m altitude which are absent at lower levels: *Quercus pallida*, *Castanea (Castanopsis) acuminatissima*, *Polyosma ilicifolia*, *Weinmannia blumei*, *Rapanea avenis*, *Elaeocarpus acronodia*, *Leptospermum flavescens*, *Eurya acuminata*, *Podocarpus neriifolia*, *Podocarpus amara*, *Acer niveum*, *Albizzia lophantha* and higher up several arboreus species of *Vaccinium* (DOCTERS VAN LEEUWEN 1933, MEIJER 1954).

HOMOGENITY OF THE SAMPLE PLOT

VAN STEENIS (1958) pointed to spot-wise regeneration in rainforest as was earlier described by KRAMER (1926) in a study of natural regeneration of montane forest in W. Java. The result of regeneration in large gaps in the forest should be a group or aggregate of individuals of one species by mere chance regeneration thus causing "local" dominance. Though this phenomenon may occur I think that it is rather overestimated and means no objection to apply "temperate" methods of analysis to tropical vegetation types as VAN STEENIS suggested.

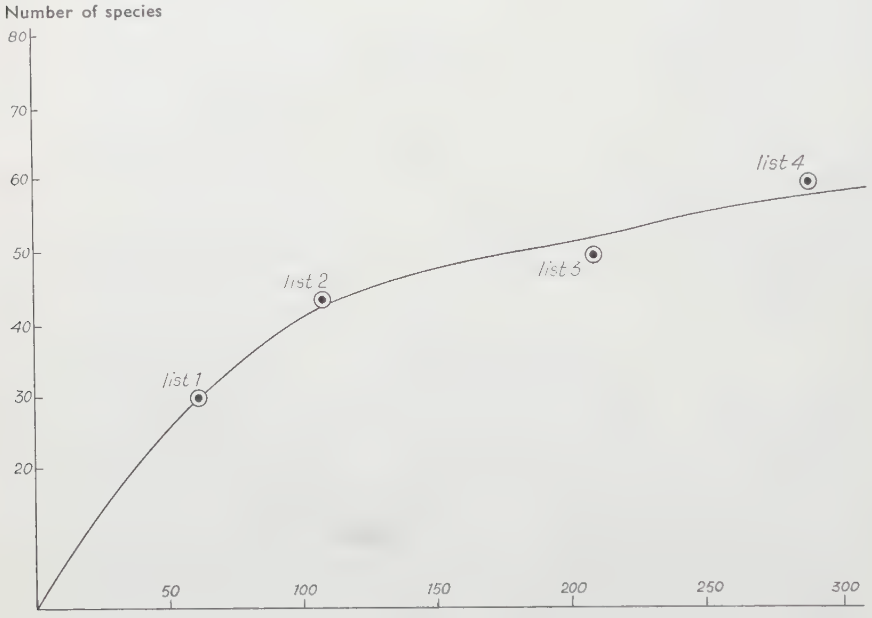

Fig. 1.

Within our sample plot some low storey trees showed gregarious occurrence. Theoretically it may be possible that such aggregates among the high storey trees escape surveys of only 1 hectare. That remains a point for future investigations.

Table II gives an impression how in certain stretches of forest within one hectare some species of trees were more frequent than others. We noted that *Macropanax dispersum* occurred especially in the south-west part of the quadrate and *Ehretia javanica* in the eastern part. *Villebrunnea rubescens* was the most frequent in the centre as well as *Saurauia pendula*. *Viburnum sambucinum* occurred in the western part. Among these species only *Ehretia* belongs to the higher storey trees. Young trees of this species were not noted within the quadrate. The other species are all lower storey trees. The same phenomenon of local gatherings was noted in the forest on Mt Sago and on Mt Kerinchi. Chance factors and the way of distribution of the species may play a part in this and local gaps always occur here and there in the forest after storms have blown down old heavy trees.

The average species composition is not so much affected by this

TABLE V

Treelets of diameter below 10 cm, occurring among the shrub layers.

A. Treelets belonging to the lowest diam. class (0–10 cm)

Talauma candolleana
Orophea hexandra
Glochidion rubrum
Allophyllus cobbe
Polyalthia
Pithecellobium montanum

B. Young trees of species which are outside the quadrate represented in the higher classes:

Hypobathrum
Litsea tomentosa
Pyrenaria serrata
Decaspermum fruticosum
Dysoxylum excelsum
,, nutans
,, alliaceum
Cryptocarya tomentosa
Podocarpus imbricata
Endiandra javanica
Michelia montana
Alangium rotundifolium
Macaranga rhizinoides
(in forest gap)

TABLE VI

The frequency of the tree species, demonstrated by the number of species represented by 1, 2–5, . . . individuals.

	number of individuals					
	1	2–5	6–10	11–20	21–30	31–40
number of species	23	26	4	4	3	1

TABLE VII

The shrub layer

A. *Treeferns, palms, bamboos and bananas*

Cyathea latebrosa
,, cf. junghuhniana
Gigantochloa apus
Musa acuminata
Pandanus furcatus
Pinanga cf. javanica
,, kuhlii

B. *Real shrubs*

Ardisia fuliginosa
,, vestita
Brassaiopsis glomerulata
Breynia laevigata
Claoxylon glabrifolium
Clerodendron disparifolium
Dichroa febrifuga
Evonymus javanica
Ficus cuspidata
,, cf. laevis
,, montana
,, pisifera
,, cf. tricolor
Lasianthus bracteolatus
,, glaber
,, purpureus
,, cf. stercorarius
Leea indica
Maoutia diversifolia
Melastoma setigerum
Mussaenda frondosa
Mycetia lateriflora
Olea javanica
Piper nigrescens
Psychotria divergens
Rapania spec
Rubus elongatus
,, fraxinifolius
,, moluccanus
Saprosma dichotomum
Schefflera rigida
Trevesia sundaica
Urophyllum corymbosum

Most prominent: members of *Araliaceae, Rubiaceae, Ardisia* and *Rubus.*
Total number: 40.
Two species *(Ficus pisifera* and *Schefflera rigida)* occur also as strangler and one *(F. laevis)* as a climber.

phenomenon in case we make our samplings at least 1 ha, or about 1,5 ha as suggested by RICHARDS (1952).

THE COMPLEXITY OF THE FOREST

This is illustrated by the high number of species in comparison with the number of their individuals, the frequency of the species, the number of different life forms sometimes even within one genus, for example in the genus *Ficus*, and by the stratification of the forest. Among 285 trees with diameters above 10 cm, 59 species occur.

Table IV gives an impression of the frequency of trees in different layers.

One species, *Villebrunnea rubescens*, is with 33 trees (11 %) the most frequent tree in this forest. It is a low storey tree, with diameters below 20 cm and according to BAAS BECKING (1948) never higher than 20 m.

TABLE VIII

Woody climbers

Calamus spec
Celastrus hindsii
Daemonorops spec.
Dissochaeta bibracteatum
Elaeagnus latifolia
Embelia coriacea
,, ribes
,, viridifolia
(Ficus laevis) [1]
Kadsura scandens
Luvunga eleutherandra
Plectocomia elongata
Psychotria sarmentosa
Sageratia ramosa
Tetrastigma dichotomum
,, cf. glabratum
,, papillosa
Toddalia asiatica
Tournefortia tetrandra
Uncaria spec.
Urceolaria javanica

[1] Species already mentioned in other life-form class.

TABLE IX

Non-woody climbers

Cissus vitigenea
Clematis leschenaultii
Melodinus spec.
Passiflora spec.
Rubia cordifolia
Smilax celebica
,, macrocarpa
Stephania capitata
Trichosanthes palmata

Stranglers

Fagraea obvata
Ficus pisifera [1]
Schefflera rigida [1]

Woody creepers

Conocephalus suaveolens
Ficus disticha
Piper baccata
Piper spec
Randia corymbosa

Non-woody creepers

Agalmyla parasitica
Ficus spec.
Freycinetia insignis
Rhaphidophora silvestris
Scindapsus hederaceus

Hemi-parasite

Scurrula korthalsii

[1] Already mentioned in the shrublayer.

TABLE X
The herb layer

A. *Ferns* (det. teste Prof. Dr. R. E. HOLTTUM)

Angiopteris evecta
Asplenium belangeri
,, cf. caudatum
,, robustum
Athyrium boryanum
Cyclosorus callosus
,, heterocarpus
,, megaphyllus
Diplazium bantamense
,, pallidum
Diplazium repandum
,, spec.
Dryopteris hirtipes
Lindsaya spec.
Marattia sambucina
Microlepia spec.
Nephrolepis acuminata
Polypodium persicifolium
Pteris spec.
Selaginella cf. opaca

B. *High herb layer*

Amomum coccineum
,, hochreuteneri
Blumea balsamifera
Coleus galeatus
Lycianthus laevis
Polygala venenosa
Strobilanthes cernuus
Zingiber odoriferum

C. *Lower herb layer*

Achyranthus spec.
Anotis hirsuta
Argostemma montana
Begonia robusta
Carex baccans
,, cf. neoguinensis
Commelina cf. obliqua
Corymborchis veratrifolia
Curculigo spec.
Cyrtandra arborescens
,, cuneata
,, picta
,, sandei
Cystorchis aphylla
Desmodium scalpe
,, spec.
Dianella montana
Disporum chinense
Elatostema cuneatum
,, macrophyllum
Elatostema sesquifolium
Eupatorium riparium
Forrestia glabrata
Impatiens platypetala
Medinilla cf. verrucosa
Ophiopogon caulescens
Ophiorrhiza cf. sanguinea
Oplismenus compositus
Paraphlomis oblongifolia
Peperomia laevifolia
Peristrophe bivalvis
Pilea angulata
Polygonum chinense
Pratia nummularoides
Procris frutescens
Sanicula europaea
Schismatoglottis spec.
Scleria spec.
Tropidia curculigoides

D. *Herbs* noted only in *forest gap*

Adenostemma macrophyllum
Eupatorium pallescens
Gynura crepidioides
Gynura sarmentosa
Pilea smilacifolia
Solanum ferox

Dominance in the herb layer

The dominant species in the higher herb layer is *Strobilanthes cernuus* (locally) while *Coleus galeatus* is rather frequent. Abundant in the lower herb layer are: *Cyrtandra picta*, *C. arborescens*, species of *Cyclosorus* and *Elatostema sesquifolium.*

The next frequent species are *Saurauia pendula* with 30 trees (max. height 20 m), *Castanea argentea* 25 trees (max. height 45,5 m), and *Altingia excelsa* 26 trees (max. height 60 m). Less frequent (between 11–20 individuals) are *Macropanax dispersum* (11 trees, max. height 33 m), *Ostodes paniculatum* (11 trees, most common in the lower storeys), *Machilus rimosa* (11 trees, max. height 31,5–40 m), and *Schima wallichii*

(11 ex., max height 43,5 m). In the frequency class of 6–10 occur in the lower storeys: *Antidesma tetrandrum* (9 trees), *Ficus ribes* (9 trees), and, in the medium storeys *Castanea tunggurut* (6 trees, max. height 43 m) and *Castanea javanica* (7 trees, max. height 58 m).

Fifteen species of trees occur in the diameter classes below 41 cm. They would not be taken into consideration by the sampling methods of the indonesian forest service in which only trees with diameters above 40 cm are included.

It is quite logical that stratification of the forest goes generally parallel with the diameter classes but every forester knows that each tree species has its own mode of growth and that we are not allowed to assume that two trees of different species with the same diameter possess the same height. From the measurements made by Baas Becking (1948) it appears that for example *Machilus rimosa* and *Engelhardtia spicata*, trees with maximal diameters between 70–90 cm, are generally shorter than trees of *Altingia excelsa* of the same diameter while at the other side trees like *Ilex pleiobrachiata*, *Acronychia laurifolia* and *Helicia serrata* possess a relative small diameter with a great height. We may thus distinguish 'plump' and 'tall' trees.

Altingia is the highest tree in this forest, the highest measuring according to Baas Becking (1948) 62 m. It is an emergent tree. (Fig. 2). Next comes *Castanea javanica* (58 m). Below this reach till about 45 m the rather frequent *Castanea argentea* and *Schima wallichii* and the less frequent *Quercus induta*, *Quercus pseudomoluccana* and the here rather rare *Engelhardtia spicata*.

Below this we meet between 20–40 m rather sparingly *Macropanax dispersum* and *Ostodes paniculata* and less frequently species of *Eugenia*, *Symplocos*, *Lauraceae*, *Ficus ribes*, *Ficus alba*, *Flacourtia rukam*, *Casearia*, *Vernonia arborea*, and very sparingly several other species.

These trees are generally low enough to name them with Field glasses on characters of leaves and phyllotaxy or to climb them in case of doubt. The higher trees have to be known by their bark and slash characters, species of the genus *Quercus* with its fissures of bark rays on its cambium, *Castanea* with a violet flush on its freshly cut cambium, *Schima* with a reddish inner bark with white needle-like fibers and a

Table xi

Total species in the life form classes

	number of species
trees	78
shrubs	40
woody climbers	20
non-woody climbers	10
stranglers	1
creepers	10
semi-parasites	1
soil herbs	73
epiphytes (Went 1940) ca	100
total	333

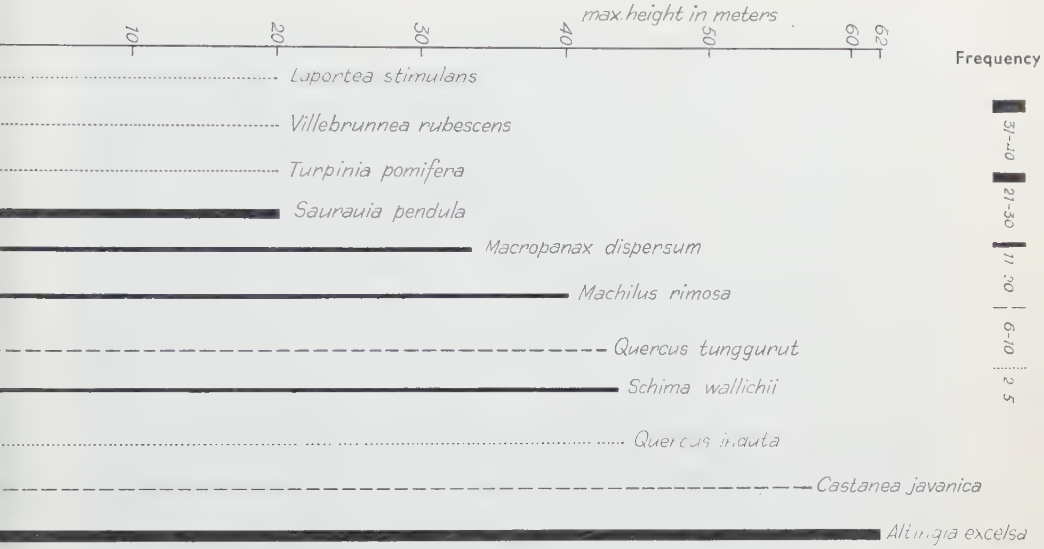

Fig. 2.

very rough fissured outer bark, *Altingia* with rather smooth scale-like bark and a distinct smell.

In forest gaps we get an impression of the stratification. In the gap in our quadrate as seen from the East we note in the foreground some treelets of *Villebrunnea*, *Saurauia pendula*, *Symplocos fasciculata* and *Ostodes paniculata* together with a young *Quercus*. Rising above this lowest storey we note a single tree of *Pygeum parvifolium* only once noticed in the whole quadrate and one of *Ehretia* of which only four occur in our hectare. Higher up in the centre we see the rather ragged crown of an old *Quercus induta*, a tree which may reach heights of 44 m, overgrown with the woody climbers *Embelia ribes*, *Randia corymbosa* and a species of *Tetrastigma*. In the background we see high trees of *Castanea argentea*. Emerging above this forest are several pillars of *Altingia excelsa*.

Fig. 2 gives an impression of the relative height of the trees and their frequency.

REJUVENATION OF THE FOREST

Our analysis gives the impression that almost all tree species noted in our survey are still rejuvenating themselves (see Table IV). Helped by the keen eyes of our local tree namers it was possible to find young plants of practically every tree species in the herb and shrub layer. A superficial first investigation of this forest would suggest that several trees occur only at the adult stage but after a thorough investigation we find very dispersed seedlings and young trees. Not a single species however has been noted with abundant seedlings. Our detailed surveys gave the following lists of young trees:

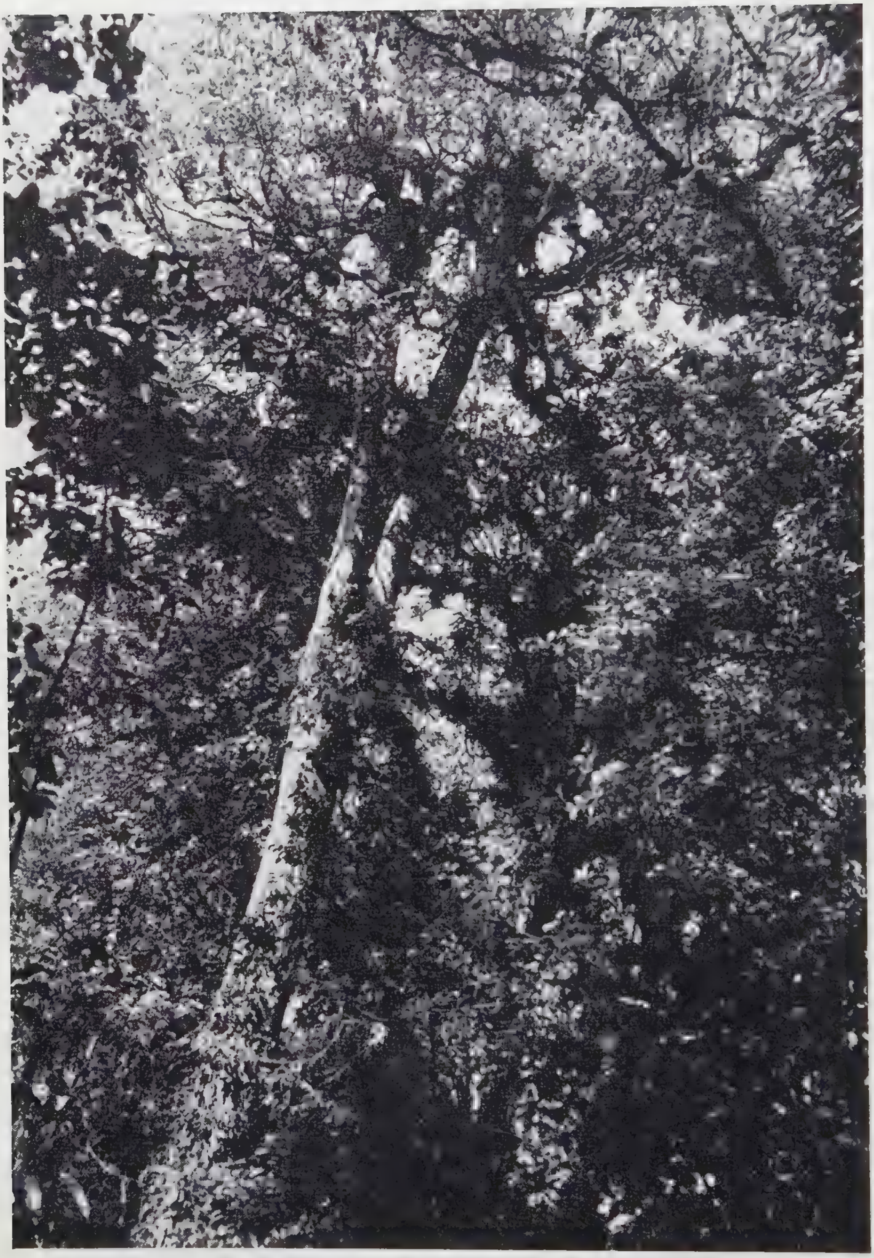

Fig. 3.
Altingia excelsa in the Tribolas Fosen (1450 m. altitude).

Plot 1

Litsea mappacea	0.5 m height	Quercus spec.	2 m height
Castanea javanica	0.5 ,, ,,	Pyrenaria serrata	3 ,, ,,
Wendlandia glabrata	2.5 ,, ,,	Symplocos fasciculata	1.5 ,, ,,
Olea javanica	1 ,, ,,	Quercus induta	2 ,, ,,
Ficus cuspidata	2 ,, ,,	Glochidion cyrtostylum	2 ,, ,,
Litsea tomentosa	2 ,, ,,	Viburnum lutescens	4 ,, ,,
Castanea argentea	3.5 ,, ,,	Ficus pisifera	2 ,, ,,
		Turpinia pomifera	2 ,, ,,

Plot 2

Symplocos costata	2 m height	Pyrenaria serrata	1 m height
Mischocarpus	3 ,, ,,	Saurauia pendula	2 ,, ,,
Villebrunnea	2 ,, ,,	Ficus cuspidata	2 ,, ,,
Eugenia densiflora	0.5 ,, ,,	Castanea tunggurut	1 ,, ,,
Macropanax dispersum	2 ,, ,,	Vernonia arborea	2 ,, ,,

Outside these 10 × 10 m sample plots the following young trees were noted:

Altingia excelsa	1 m height	Helicia serrata	1 m height
,, ,,	0.03 ,, ,,	Podocarpus imbricatus	0.05 ,, ,,
Schima wallichii	0.5 ,, ,,	Glochidion rubrum	2 ,, ,,
Casearia coriacea	1 ,, ,,	Dysoxylum alliaceum	2 ,, ,,

From the studies made by KRAMER (1926) on the forest rejuvenation of Mt. Gede outside the nature reserve we may conclude that seedlings and young trees develop much more numerously when gaps occur in the forest. Moreover species of *Strobilanthus*, *Zingiberaceae*, *Cyrtandra* and *Elatostema* get a better chance to form dense vegetations. When these gaps become big, however, tree species typical for secondary forests become dominant. The only distinct example of such a tree in our sample is *Macaranga rhizinoides* in the above mentioned forest gap. The biggest changes after tree felling occur in the herb layers where species like *Gynura crepidioides*, *G. sarmentosa*, *Eupatorium pallescens*, *Adenostemma macrophyllum* and *Blumea balsamifera* become abundant (Table X). Such vegetations are possibly to be compared with "Hochstaudenflur" of temperate forest gaps. The occurrence of these species possibly depends not only on a change in the light factor but also on microbiological activities in the soil connected with greater humus decomposition. Concurrency for young trees seems to be difficult in cases where a dense "secondary" herb layer is developed.

AGE, DEGRADATION AND RENEWED SUCCESSION

As a result of tree measuring executed by KOORDERS (1914), BRUGGEMAN (1927) and BAAS BECKING (1948) extending over a period of 34 years, BAAS BECKING (1948) estimates the maximum age of trees in the Tjibodas forest to be between 200–250 years, the mean average of the measured trees 130 years, the mortality 0,77–0,83 % in each year. The last figure is important in order to know how much "harvest" such a forest can stand without almost any change in composition when only fallen trees or quite dispersed very old trees are removed.

When indiscriminate exploitation takes place the growth of the young tree generations is accelerated and accordingly the opportunity for a greater harvest (Kramer 1926); when the exploitation is carried out according to a wise policy of very dispersed tree felling the forest structure is left intact.

In the case of a harvest which is too big the rejuvenation is hampered and the quality of the forest decreases because its character is changing into the direction of secondary forest with many tree species with very soft wood. A detailed understanding of these processes are highly useful in forestry practice. A long experience with tree species and forest composition is necessary before a forester is able to handle the forest in the wisest way possible.

Ecological remarks

The ecological character of the forest in this sample plot appears most clearly from a study of the spectrum of the life forms (Table XI). This montane forest has a cool wet climate with average temperature 17.7° C (extremes 12–27° C), rainfall 3400 mm, relative humidity 80–90 % [1]) and a maximal dry period of three weeks (Went 1940). This climate is reflected by the rich development of epiphytes, the relative poorness of woody climbers and the rich vegetation of soil herbs. Lowland rain forests are known for their poor terrestrial flora and the lack of a well developed humus layer (Mohr and van Baren 1954), epiphytes are generally also less luxuriently represented in the lowlands, except near rivers. The soil in our sample plot is formed by the deposits of the volcano, Mt. Gede. A soil profile showed us that the layers which are rich in humus reach a depth of about 20–30 cm and that the hard rocks lay at about 70–80 cm below the surface.

Several soil herbs like members of the genera *Cyrtandra*, *Elatostema*, *Begonia* and *Strobilanthes* (sensu lato) which are rather abundant in our sample plot may be considered indicators of a rich soil, not deficient of mineral salts. To my experience in forests in Borneo and Sumatra they are always lacking on poor sandy acid soils, and less abundant on old or originally more acid than on young rich volcanic soils.

SUMMARY

After three years of continued botanical study of the flora in the nature reserve of Tjibodas, Mt. Gede, W. Java it appeared technically possible to make a total inventary of a homogenous part of the mountain forest at about 1500 m. altitude in which all trees with diameters above 10 cm at breathheight were named and counted. It appeared that such an intensive study of a relative small part of the forest of Mt Gede comprises the bulk (about three quarter) of the flora of the montane region (1400–1700 m. alt.). The higher layers of the forest are chiefly composed by oaks, chestnuts, *Altingia* and *Schima* while especially *Lauraceae* and species of *Eugenia* come to the fore in the lower storeys. Half of the tree species represented in the sample plot occurred only once. About 13 tree species were only found in juvenile state. The more common species are represented by younger stages in all size (age) classes. Some species show local gatherings which possibly depend on their way of distribution. The total inventary of the flora on one hectare comprises about 333 species of phanerogams and ferns, including 78 species of trees,

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[1]) My own measurements on 2 August 1955 were 10 a.m. in halfshade in forest: temperature 17° C, relative humidity 90 %, during one day and night in rest house max. temp. 27° C – min. 13° C.

40 species of shrubs, 73 species of soil herbs and about 100 species of epiphytes. The latter groups especially reflect the montane character of this forest and among the soil herbs occur species which might be considered as indicators of the fertility.

The study must be considered as a first attempt to apply modern methods of plantsociological analysis in the mountain forests of Java.

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REFERENCES

BAAS BECKING, L. G. M. 1948. Notes on jungle trees 1. Chron. Nat. **104**: 271–277.

BRUGGEMAN, L. A. 1927. The numbered trees, shrubs and lianes in the forest of Mount Gede near Tjibodas, West Java. Bull. Jard. Bot. Btzg. III, **9**: 196–219.

DOCTERS VAN LEEUWEN, W. M. 1929. Tjibodas (Botany) (Exc. Guide C 3, 4th Pac. Sci. Congress, Java: 3–17). Repr. in Honig & Verdoorn, 1945, Science & Scientists in Neth. Ind.: 409–413.

————. 1938. Biology of plants and animals occurring in the higher parts of Mt. Pangrango-Gedeh in West Java. Verh. Kon. Akad. Wet. A'dam. 2e Sect. **31**: 1–178.

KOORDERS, S. H. 1914. Floristischer Ueberblick über die Blütenpflanzen des Urwaldes von Tjibodas etc. Bot. Jahrb. **50**: 278–303.

————. 1918–1923. Flora von Tjibodas. Batavia.

KRAMER, F. 1926. Onderzoek naar natuurlijke verjonging en den uitkap in Preanger Gebergebosch. Thesis. (also publ. in Med. Proefdat. Boschw. 14, 1926).

MEIJER, W. 1954. Plantensociologische waarnemingen in de top-regionen van Gedeh en Pangrango. Penggemar Alam **34**: 9–17.

MOHR, E. C. J. and F. A. VAN BAREN. 1954. Tropical soils. The Hague.

RICHARDS, P. W. 1952. The tropical rainforest. Cambridge.

STEENIS, C. G. G. J. VAN. 1958. Basic Principles of Rain Forest Sociology. Proc. Kandy-Symposium Unesco: 159–165.

———— and M. J. VAN STEENIS-KRUSEMAN. 1953. Brief sketch of the Tjibodas Mountain Garden. Flora Mal. Bull. **10**: 313–351.

WENT, F. W. 1940. Soziologie der Epiphyten eines tropischen Urwaldes. Ann. Jard. Bot. Btzg **50**: 1–17.

————. 1945. A naturalist's Paradise, in Honig & Verdoorn. Science and Scientists in Neth. Indies: 403.

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A PRELIMINARY NOTE ON THE PLACENTA OF STELLARIA MEDIA (L.) VILL. AND STELLARIA GRAMINEA L.
A POSSIBLE AXIAL ORIGIN OF OVULA?

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(received March 31th, 1959)

INTRODUCTION

The different types of gynoecia can be explained by those, who consider the carpel as an infolded foliage leaf, which develops ovula at the margins. This typo-morphological conception is supported by most botanists. This theory, also called the appendicular theory, goes back to A. P. de Candolle.

In fact the appendicular theory leans on the vascular anatomy, a method, founded by VAN TIEGHEM (1868; 1875) and employed with much success by Eames and his school, for the interpretation of the flower. In this theory, the central placenta is a much discussed subject, which caused a good deal of research. In many cases the central placenta of the Primulaceae has been the motive. All this work centered upon the question whether the central placenta is wholly or partly formed by carpellary tissue. In a well documented article PURI (1951) states, that "the central region of the column is axial, while its peripheral region which bears the ovules is carpellary".

Typologically the Primulaceae gynoecium may be derived from the Caryophyllaceae by further reduction of its septa, since we can state that in several genera of this family the septa may vanish in later stages of its ontogenetical course. Moreover, this opinion is supported by the facts, known from vascular anatomy. (DOUGLAS 1936; DICKSON 1936; THOMSON 1942).

ECKHARDT (1954; 1955) states in his work on the Centrospermae with basal ovules, that these are formed by the carpels, namely as a product of the "querzône", where also the vascular anatomy had to supply the evidence.

Starting from the idea of the infolded foliage leaf, LEINFELLNER (1950) states that the Caryophyllaceae placenta is formed by the basal and marginal parts of the carpels; in his terminology: by means of the symplicate and synascidiate parts of the syncarpous gynoecium. This opinion however, is not the same as that of SCHÄFER's (1890), who thought that in the more-seeded Caryophyllaceae gynoecium the basal part of the placenta is not formed by the basal part of the carpels but by the carpel-margins. In Troll's terminology: the carpel may be epeltate.

On the contrary, the other opinion states, that the ovules are not a product of the carpel-margins, but just axial products.

Payer (1875) thought this to be sound for all ovules. In her work on the vascular anatomy of the Primulaceae, Douglas (1936) has published a wellwritten review of the authors supporting the axial nature of the ovules. These authors willingly admit that the placental column is partly formed by carpel-margins or -bases, but insist on the axial origin of the ovules. Especially those investigators working with fossil material and several historical-orientated workers are likely to held this opinion.

Recently this controversion gave birth to a renewed vivid discussion, caused by a series of publications by Lam (1947–1955). The paleobotanical idea of axial and folial sporangien was adapted by Lam for his conception concerning the phylogeny of the cormophyta. Lam suggested, that the angiosperms could be derived from two stocks, namely the phyllo- and stachyospore plants. The Centrosperms could well have been of stachyosporous origin.

Lam's publications have aroused much opposition, because his ideas are controversial to the classical idea of the carpel and the probable origin of the angiosperms. (Eames 1951; Eckhardt 1954; 1955).

From an investigation into the ontogeny of flower phylloms in some Stellaria species, I was struck by the way the placental column is formed. This investigation might probably be a small contribution for a further discussion concerning the nature of the problem I stated in my introduction to this article.

Materials, methods and observations

The floral diagram and the position of the symmetrical plane of Stellaria species has long been misunderstood. The carpel orientation with respect to the sepals is presented in different ways, to begin with Wydler (1851). In 1932 Matzke published an elaborate study about *Stellaria media*, in which he stated, that an equal number of flowers with sepals originated in clockwise sequence as well as in counterclockwise sequence. This phenomenon is reflected in the carpel orientation.

Contrary to the other authors Matzke demonstrated that the symmetrical plane goes through sepal number 4 and between sepals number 3 and 5. (Fig. 1).

Although I haven't used as many flowers as Matzke had in his investigations, I agree with his findings.

1st Method. Flower buds of different age, put into diluted glycerine, are examined through a binocular microscope. This method has been excellently employed by Payer (1857), and as to Caryophyllaceae tribus Alsinae, especially with regard to the placenta, by Lister (1883).

After the sepals have been formed in a quincunx, clockwise or counterclockwise, the episepal anthers are formed. Then the epipetal anthers are formed. When these latter primordia have formed hill-like shapes, there still is left a dome-shaped column, the future placenta. Meanwhile at the base of the column emerges a ringwall: the carpels.

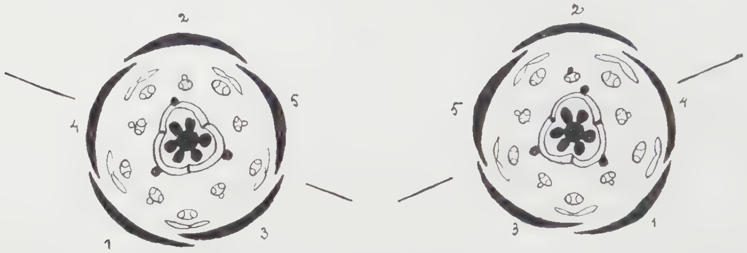


Fig. 1. Floral diagram of Stellaria media. The clockwise and the counterclockwise form; showing the symmetrical plane of the flower (after MATZKE).

In a later stage of the growth of the carpels, I detected small and delicate ridges pointing upwards the ringwall into the direction of the top of the column: the future septa. Only then the situation named by Lister in her article is achieved.

According to BAUM (1950) we may have here the forming of congenital fused carpels, quite in contradiction to Lister. When these carpels have grown half the height of the column, the ovules are formed; starting at the top these ovules are situated next and apart from the septa.

Before the forming of the first ovules the petals emerge from an own primordium as small transparant protrusions directly behind and at the base of the epipetal anthers, provided they exist; since *Stellaria media* frequently has less than ten anthers. The fast growing sepals quickly envelop the other floral phylloms.

From these observations concerning gynoecia, the following questions can be raised:

1. When the carpels from their primordia are formed and still there is a dome-shaped column mass, could it be possible that this column tissue is partly formed by carpel tissue in its peripheral zone, or could this be a direct prolongation of the stem?
2. When the ovules are formed whilst the carpels are not yet fully developed, (that is, when the ringwall has not yet reached the height of the column), and where the septa are hardly detectable, could they be able to form the ovules in the manner as the classical theory states?

To give an answer for above mentioned questions, I had to use normal microtome technics, since the first used method can only be applied for examining the outer sides of the floral phylloms.

2ND METHOD. Dichasia from *Stellaria media* and *Stellaria graminea* were embedded in paraffine, sectioned serially at 10 microns, stained in Delafield haematoxyline (for plasma staining) and in haematoxyline according to Regaud + saffranin. Complete series were studied, transverse and longitudinal.

In this manner series of different flower stages could be obtained. The histogenetical pattern of cells of the flower phylloms were studied. The same sequence of ontogenetical development is observed as before with the first method by using a binocular microscope.

On account of recent histogenetical research concerning the flower, to begin with GREGOIRE (1937) and especially by the newest findings of PHILIPSON (1947), BUVAT (1952) and BERSILLON (1955) and others, the conception considering the forming of the flower has changed. For an insight into this matter I refer to the publications of the authors mentioned above.

The opinion of Buvat and his followers with respect to the forming of the flowers, I can agree with. Namely, that the flower apex consists of a cap of two layers. The cells of these layers are big and darkly stained in my microscopical slides; proméristème sporogène — (Buvat).

Here beneath lies a core formed by cells which divide principally anticlinically = proméristème receptaculaire (Buvat). The subepidermic layer is active in forming the floral phyllomes, except the sepals. I will go in details in an other paper in respect to this problem.

Photograph 1. Gives a longitudinal view of a flower bud. Here we see a detail of the gynoecium of a young flower of *Stellaria graminea*. On the left and on the right hand side of the picture are anthers. In this section a petal primordium is slightly cut up which can be noticed at the base of the right hand anther. Between the anthers is situated the flower apex, the future placental column, which for convenience' sake we will call just "column". At both sides of the column's base we see carpels. The left one is nearly cut in the midst. In this part we can see the active topcell which divides peri- and anticlinically. The two outer layers of the column are dark stained while the rest of the column tissue is made up by ribmeristem.

Figure no 2 is a drawing of a detail of a longitudinally cut young gynoecium of *Stellaria graminea*. On the left side, a carpel is cut through the septum. On the right side a carpel is cut through about the midst.

Figure no 3 is a drawing of a longitudinally cut young flower of *Stellaria graminea* in a later stage of growth. In this drawing, the left carpel is cut through about the midst, while the right carpel is cut through the septum. This figure is a transection through the symmetrical plane of the flower, because we see on the left side a petal primordium with its epipetal anther and on the right side we see an anther which is bigger than the other one: an episepal anther. From the floral diagram as it is given by Matzke and agreed upon by me, it is clear, that a plane as described above can only be the symmetrical plane.

When we look at a series of details of this young gynoecium represented by photographs 2 7, from which photograph no. 2 corresponds with Fig. 4, photograph no. 5 corresponds with Fig. 5 (which is a detail of Fig. 3) and photograph no. 6 corresponds with Fig. 6, we observe on this series the following facts:

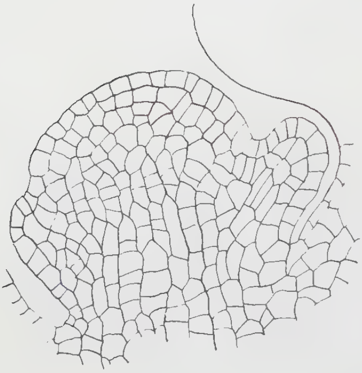


Fig. 2.

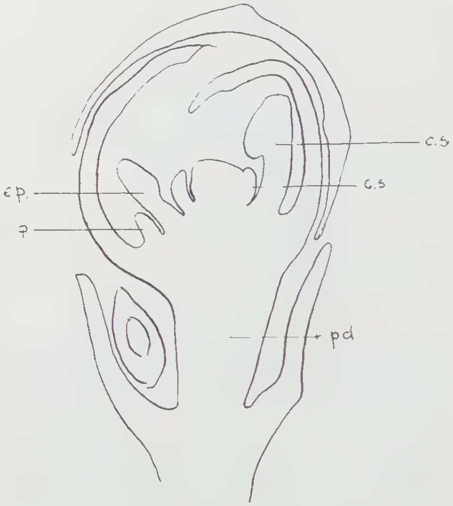


Fig. 3.

Fig. 2. Stellaria graminea. Longitudinal section through a young gynoecium. At the left side of the column, the section goes through the margin of a carpel primordium. In this place the future septum will be formed. At the right side of the column, a carpel is cut through the midst.

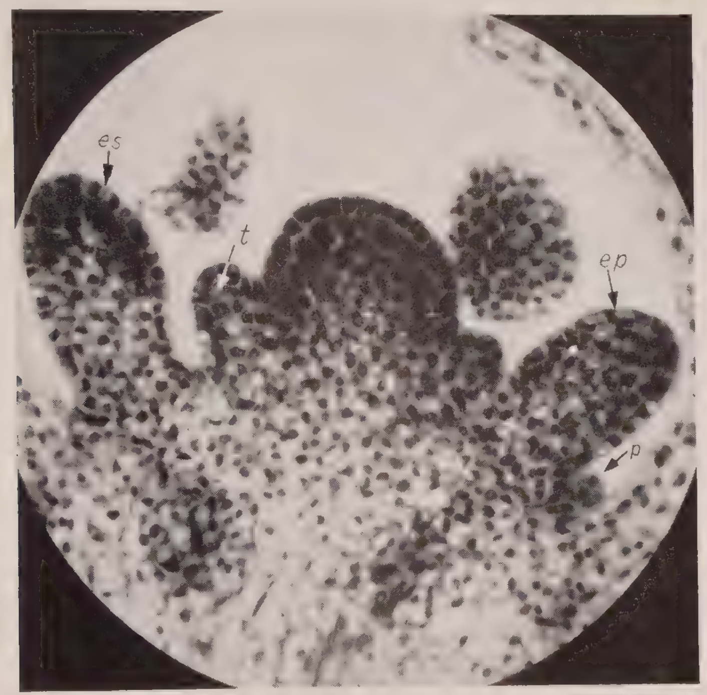
Fig. 3. Stellaria graminea. A drawing of a longitudinal cutting of a flower, through the symmetrical plane. (see text). Left carpel is cut through the midst, the right one through its septum. ep = epipetal anther; es = episepal anther; p = petal; cs = carpel septum; pd = peduncle.

We see the caesura between column and right hand carpel reduce, which means, that the cuttings are approaching the septum. In photograph 4 and 5 the septum is reached and in photograph 6 and 7 we have entered the next locus, which is to be seen on the growing caesura. On the contrary the caesura between column and left septum is deepening, this indicates that we are going into the direction of the middle of the carpel.

In Fig. 4 we see that the column is flattened at the top, a beginning of the forming of the ovules has started, while at the leftside base of the column the forming of the ovules is yet about to begin.

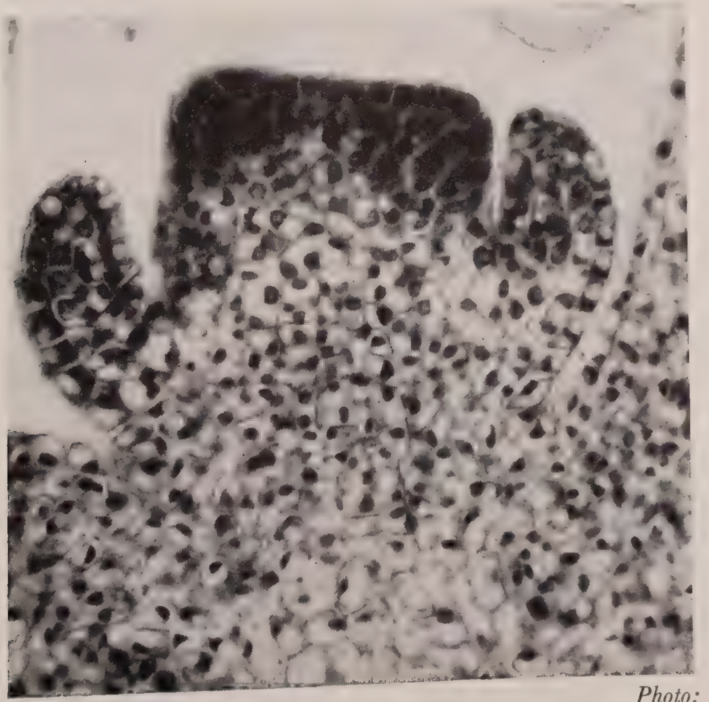
This younger phase of ovule forming on the left side of the column can be better seen on photograph no. 3.

In Fig. 4 we see again the two layers of dark stained cells forming the cap of the column, while the rest of the column tissue is made up



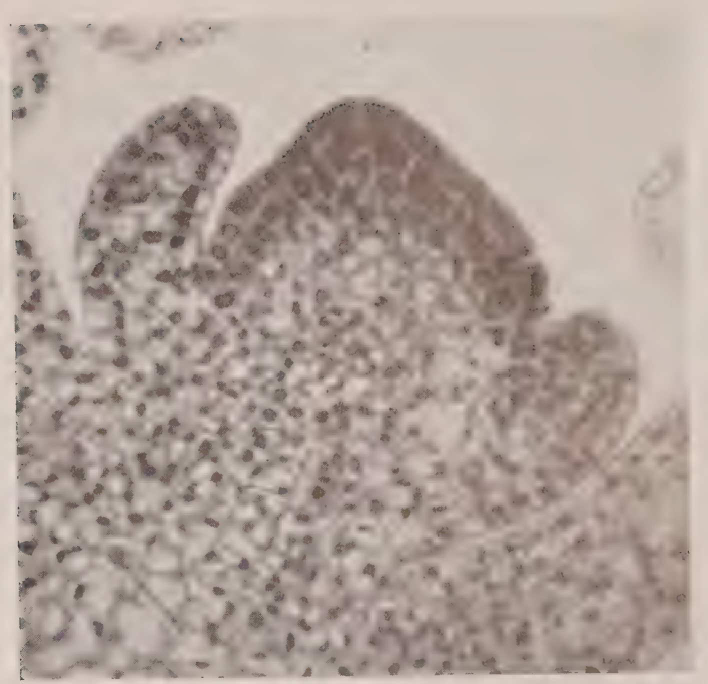
Photograph no 1 *Photo: F. J. Smith*

Stellaria graminea (L.) Longitudinal section through a young gynoecium. es = episepal anther; ep = epipetal anther; p = petal primordium, just slightly cut; t = topcel of carpel primordium. The two-celled tunica layer is dark stained and bigger than the other cells. Stained with Delafield's haematoxyline.



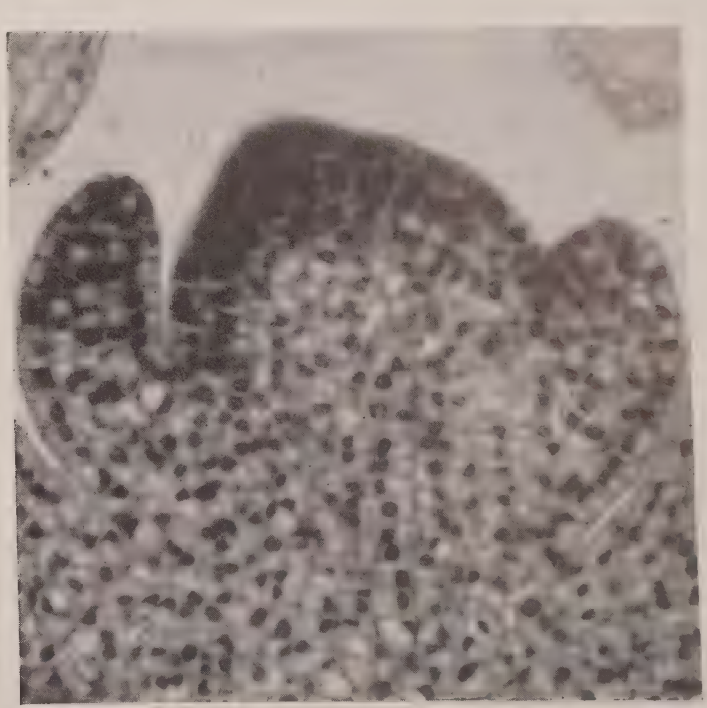
Photograph no 2 *Photo: F. J. Smith*

Stellaria graminea. The photographs 2–7 are details of a series of cuttings through a young gynoecium. Photograph no 2 presents at both sides of the top the differentiation of the ovules (→).



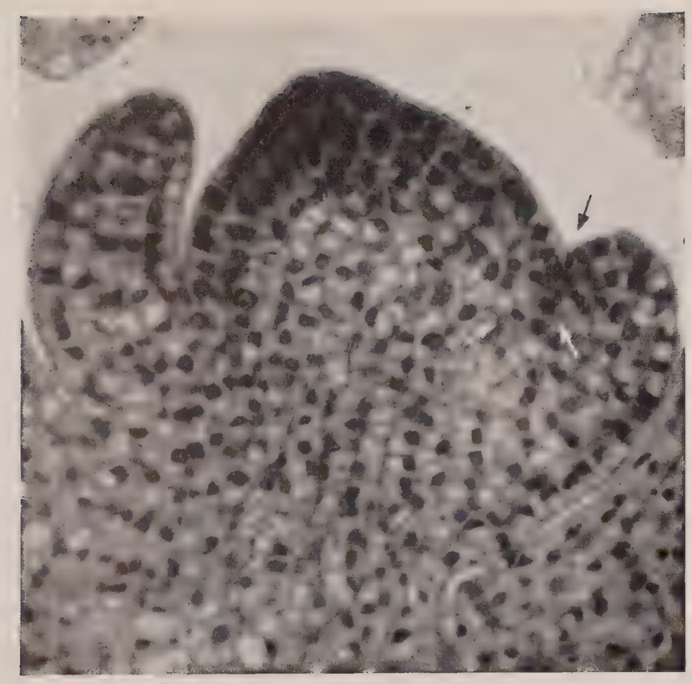
Photograph no 3 *Photo: F. J. Smith*

Stellaria graminea. At the left side of the column we can see the differentiation of a basal ovule. The right side carpel is fused with the column, higher than in the preceding photograph.



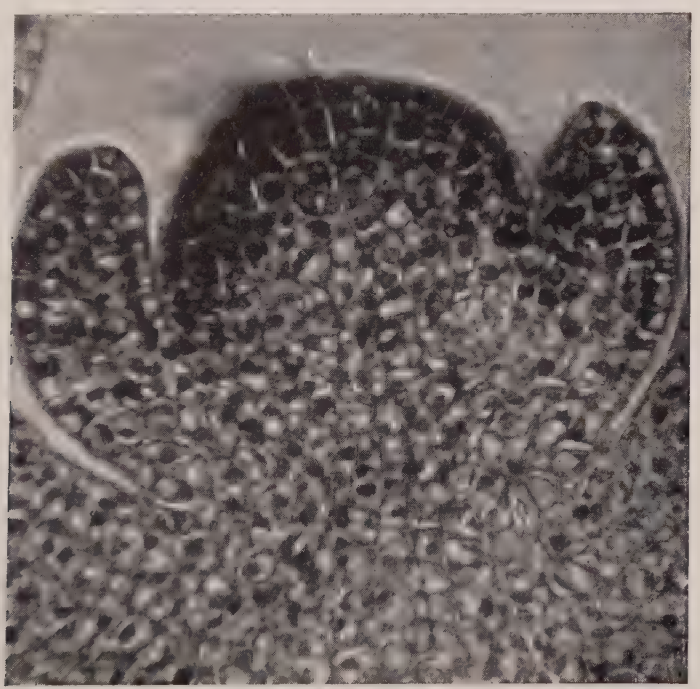
Photograph no 4 *Photo: F. J. Smith*

Stellaria graminea. Photograph no 4 and no 5 are details of Fig. 3 Photograph no. 4. The cutting is through the symmetrical plane. Here we notice, that carpel margin tissue is just slightly penetrating the column tissue.



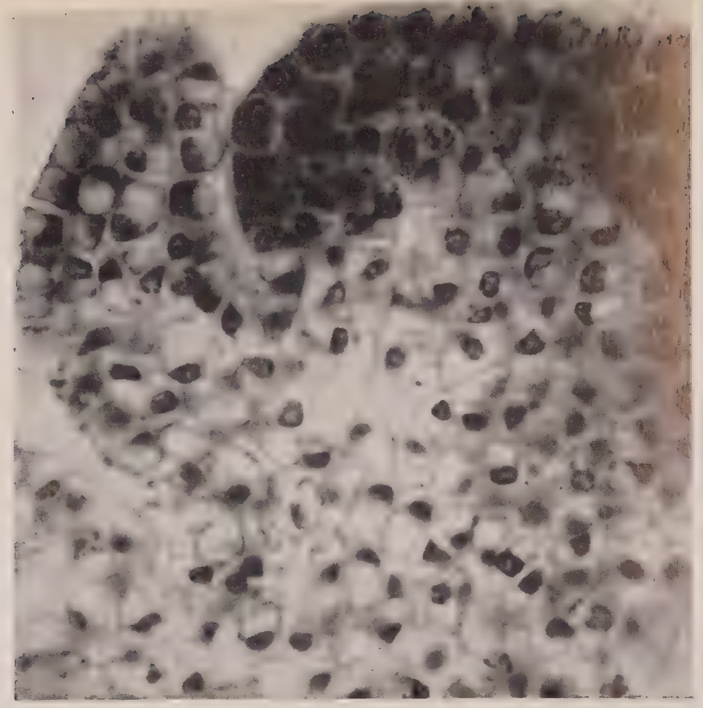
Photograph no 5 *Photo: F. J. Smith*

Stellaria graminea. Photograph of the same section as no 4, but taken with a focus deeper than that one. The borderline between column and carpel margin tissue is noticeable (Fig. 5).

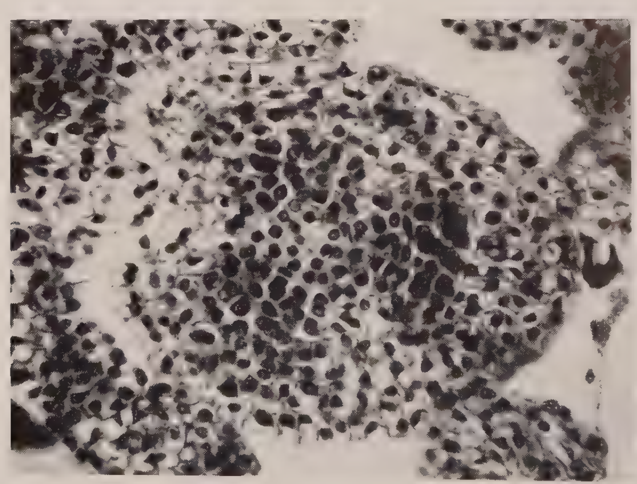


Photograph no 6 *Photo: F. J. Smith*

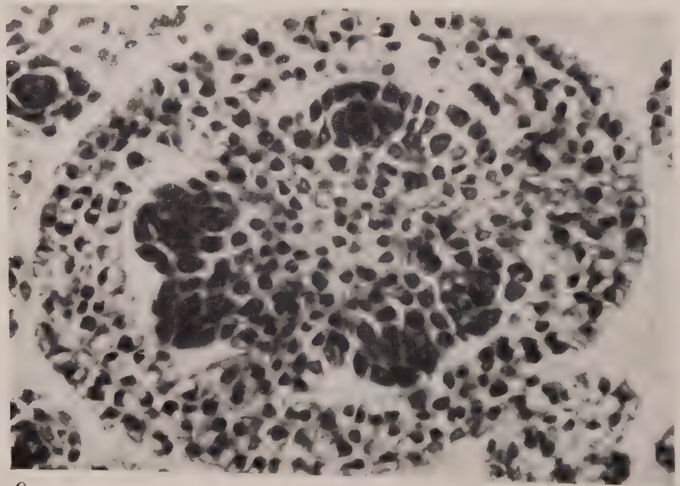
Stellaria graminea. The separation between right carpel and column tissue can here be noticed again; we have arrived into another locus. (Fig. 6). Taken with "phase contrast".



Photograph no 7 *Photo: F. J. Smith*



Photograph no 8 *Photo: F. J. Smith*



Photograph no 9 *Photo: F. J. Smith*

by the proméristème receptaculaire demonstrating a well outlined pattern of the cells of cambial nature. The growth of the carpels on the left and right side of the column doesn't interfere with column tissue.

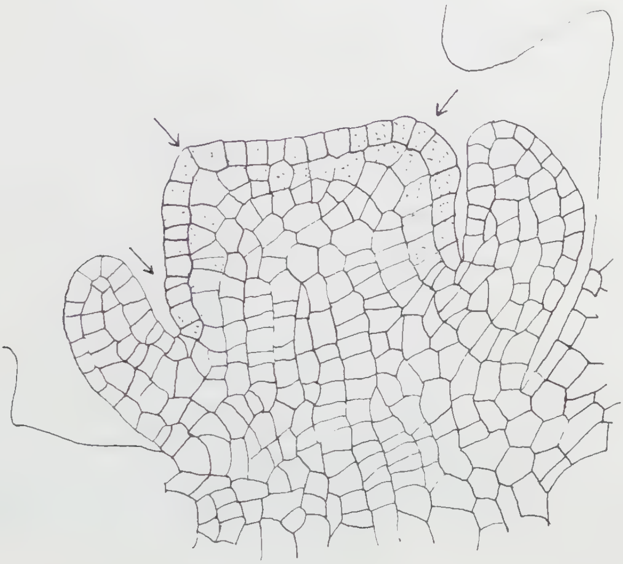


Fig. 4. Stellaria graminea. Drawing of the same cutting as represented in photograph. 2. A detail of a young gynoecium. Notice the flattened top of the column while at both sides ovula forming starts (→). Here too we see the regular pattern of anticlinally devided cells of the core (ribmeristem).

Photograp no. 4 and no. 5 (= detail of Fig. 3) are pictures of the same section, taken with different depth of focus. In these pictures the septum of the right side carpel is fused with the column tissue. Photograph no. 4 shows that the septum of the right side carpel is just slightly penetrating the column tissue, while photograph no. 5

Photograph no 7

Stellaria graminea. Detail of the left carpel of carpel, seen in a cutting next to the one presented in photograph 6. Carpel tissue lightly stained, column tissue dark, (see text).

Photograph no 8

Photo 8 and 9: Stellaria media. Details of transverse sections through a young gynoecium. Photo 8: The basal ovules are just differentiating, in the 3 loci, no vascular tissue is detectable.

Photograph no 9

Transverse section of the same gynoecium as in photo no 8, near the top of the column. The cutting goes through the older ovules. We see in each locule 2 ovules forming. No vascular tissue is detectable. Neither of both photographs shows the demarcation of carpel and column tissue.

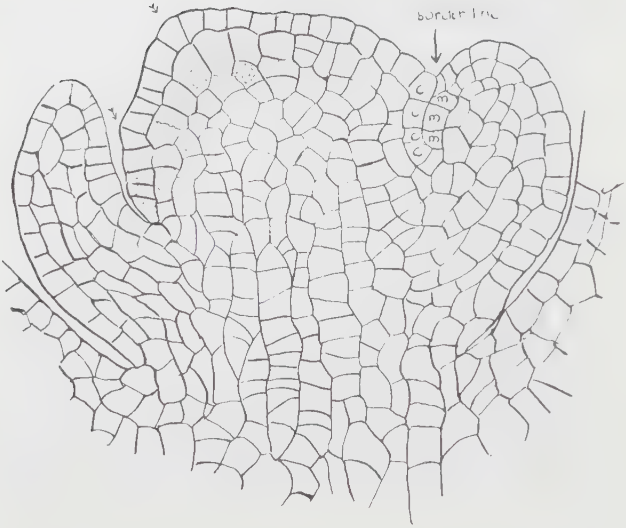


Fig. 5. Stellaria graminea. Drawing of the same cutting as represents photograph no 5. The cutting goes through the gynoecium in the symmetrical plane of the flower. Left carpel is separated from the column. The vaulting in the column (→→) indicates the places, where ovule differentiation has started. Septum of the right carpel has fused with column tissue. However, its borderline is detectable by the pattern of the margin tissue cells of column and septum. c = column cells; m = septum cells.

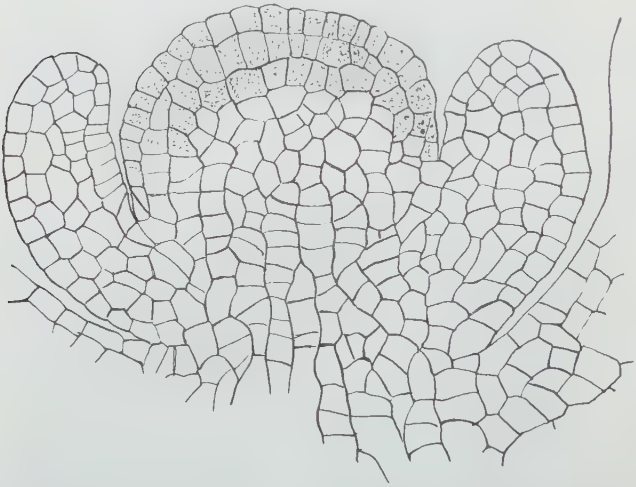


Fig. 6. Stellaria graminea. Drawing of the same cutting as represented in photograph 6. Explanation: see at that place.

shows that the outer cells of both column and septum are fused. This situation is drawn in Fig. 5. Although we can in that figure notice that the edges of column and septum tissue are fused, we still see in their histogenetical pattern (cells "c" = part of column tissue; cells "m" = marginal septum tissue) the borderline between septum and column. So we have here an apposition of the septum against the column. Hereby carpeltissue doesn't contribute to the peripheral zone of the column nor gives birth to the ovules.

Photograph no. 6 (= Fig. 6) represents a next cutting in the series. It shows that the right side carpel and the column are separated again. This means, that we have arrived from the septum into an other locus.

Photograph no. 7 is a detail of the left side of the cutting next to photograph no. 6. We see the left side carpel with its septum (lightly stained) against the dark column tissue. The septum seems to grow up against the column, but I think I have demonstrated already that carpel tissue and column tissue stay separated.

Figure 7. Represents the situation of a gynoecium which is a few older. The carpel have grown up higher, but the column too. This column bears at both sides of the figure two ovules. The figure is made from a cutting through the peripheral region of the column.

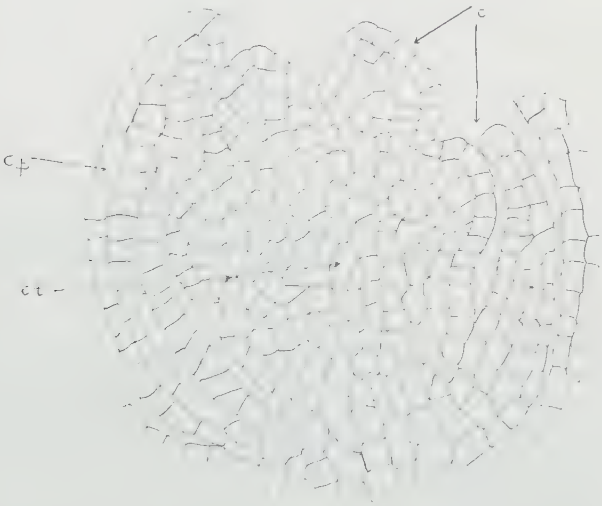


Fig. 7. Stellaria graminea. A detail of the longitudinal cutting through an older gynoecium than represented in the preceding figures. Carpels and column have grown up higher. (see text). Cp – carpel wall; ct – column tissue; o – ovule.

Placentation

Puri (1952) has published a well written article on the placentation in Angiosperms. His interpretation on this subject centered upon the vascular anatomy. For the marginaxile (according to Sachs, 1882) or axile type of placentation of the other authors, the common placental type of the Caryophyllaceae, Puri states that the infolded carpel of this gynoecium have 5 traces, from which the ventrals are inversed.

Thomson (1942) has already demonstrated that for some genera of this family, including *Stellaria* no inversed traces in the placental column are found.

I observed that at the base of the ovary the vascular tissue forms a hexagonal core with a lobe at each corner (Fig. 8). These six lobes give at different heights of the bottom of the gynoecium traces, namely the three dorsal medians and the three median laterals. These median lateral, according to the classical theory, are of a double nature.

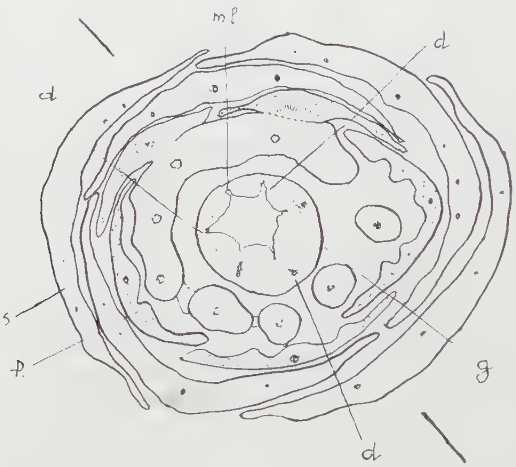


Fig. 8. Stellaria graminea. Drawing of a transverse section through the base of the gynoecium of a flower. The six vascular traces, who supply the carpels are to be seen. s — sepals; p — petal; g — gynoecium; d dorsal trace; ml median lateral trace.

When the gynoecium has grown up sufficiently (i.e. when seedforming is about to start) these traces often are found to be trifurcated at the bottom of the carpel wall; sometimes hereby the neighbouring side-traces fuse, while the middle ones stay alone.

Thomson stated that the placental vascular supply forms a core with three lobes directed towards the loculi.

Because most investigators on this subject are looking chiefly on transverse sections, and focus their attention to the vascular anatomy, they are not able to detect the separation of column tissue and carpel-tissue.

Photograph 8 and 9 give such a transection through a young gynoecium of *Stellaria media*. Photograph 8 gives a situation at the lower part of the column. Hereby, the younger ovules are not that much differentiated as the higher situated ones, visible in photograph 9. In both photographs we cannot see the borderline between septum and column tissue. I must agree, that there are some differences in outlook of the transverse section of *Stellaria media* and *Stellaria graminea* but there is no principal difference.

The vascular tissue develops rather slowly in the column tissue (photograph 8 and 9). The ovuleforming has started, but still no signs of any vascular development can be detected.

The vascular bundle development begins at the base and goes upwards in the already mentioned three edged core, starting at the corners. In the beginning more phloem is formed than xylem. The tissue between those three strands is differentiated afterwards into vascular tissue, so that at least the three-edged core is completed. Afterwards from these three corners the placental traces originate, and become fused with the ovules.

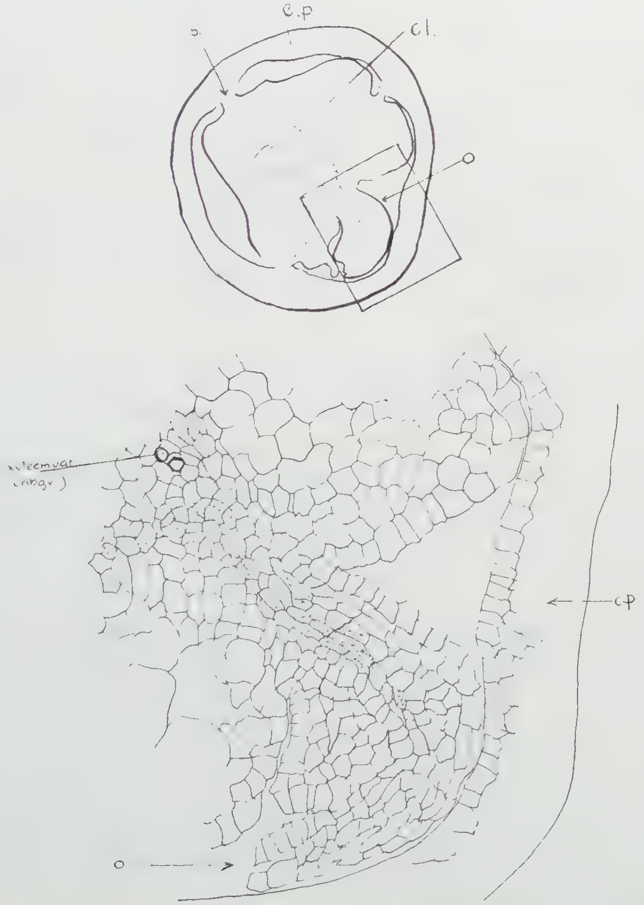


Fig. 9A and 9B. (Fig. 9B is a detail of 9A). Transverse section of the same flower of figure 7, through the base of the placental column, showing one ovule formed in a locus. Placental trace develops from column tissue (in drawing dotted). cp = carpel; s = carpel septum; cl = column tissue showing the three edged core of vascular tissue; o = ovule, differentiated from column tissue.

Figures no 9A and 9B (9B is a detail of 9A) show a differentiation of the columntissue into a trace from the ovule into the vascular core. This means that the placenta is also formed like the ovules from column tissue. In later stages the regular pattern of the vascular tissue in the column is disturbed by the growth of the different parts within the carpels, as e.g. is the case with the irregular number of ovules which set to seedforming.

CONCLUSIONS

The results, obtained by means of a histogenetic way of working, show that the idea of the placental column, partially or wholly covered with carpellary marginal tissue in which this very carpellary tissue bears the ovules, is contestable. The "carpels" are formed similarily as a sessile leaf where no "querzône" is detectable. (Troll would call this "epeltat"). The margines of these "carpels" are fused and form the later septs. In spite of the fact that the margins of the "carpels" seem to be changing gradually into placental column tissue, in reality we can prove the border between the placental column tissue and the "carpel" margin tissue. By the pattern of the cells this border is recognised.

The septa are intact until the embryo-sack stage is reached. In later stages, the septum becomes delicate and fragmentary, even disappears completely (Thomson has also stated this).

As to the placental column, we see it enlargen while the dome-shaped top flattens.

Then ovula forming starts. The first are formed at the top, hereafter the others are formed. The small xylem strands in the centre of the placental column which Thomson has interpreted as stemrests is a misinterpretation.

The much contested axile placentation in the *Stellaria* species I examined proved to be a direct elongation of the stem, it is formed by a two cell thick tunica layer, theproméristème sporogène; and a core of promérisième receptaculaire. The very cells of the second layer of the proméristème sporogène which by means of divisions give the birth to the ovules.

In how far these conclusions are appliable to the tribus Alsinae or even to the whole family of the Caryophyllaceae, is still a question, since BERSILLON (1955) in his work about the floral morphology in some genera of the family of the Papaveraceae didn't get similar results. Therefore, we have to be careful. In my opinion, however, the histogenetical method has proved that from the ontogeny we cannot in fact find any sign for an eventual phylogeny, nor signs of primitive characters. The floral phylloms are so formed that their final form of its own accord is developed from the primordium. This is the meaning of BAUM (1950) too.

It is quite alluring to consider the "carpel" in the classic meaning of the word now as a pseudocarpel HAGERUP (1933), LAM (1947), EMBERGER (1944), FAGERLIND (1958).

Since in present days the discussion about the subject is still very vivid, it seems wise to me, with the limited results I obtained, not to go into speculations about it. However, for the telom theory according to Zimmermann (1949) the facts I found are not necessarily something extraordinary. For, according to this theory, leaf and axis are to be led back to "ground telomes" the flower as a whole being a complex of syntelomes.

Anyhow, it is clear, that those are right, who are pleading to broaden the conception of the carpel, as it is since the time of Goethe, defined by the typological way of consideration.

REFERENCES

Arber, A. 1933. New Phytol. **32**: 231–242.
———. 1937. Biol. Rev. **12**: 157–184.
Bailey, I. W. 1949. J. Arnold Arb. **30**: 64–70.
Baum, H. 1948. Oestr. Bot. Zeits. **95**: 86–94; 95: 125–128.
———. 1949. Oestr. Bot. Zeits. **96**: 64–82.
———. 1950. Oestr. Bot. Zeits. **97**: 333–341.
Bersillon, G. 1955. Ann. Sc. Nat. **16**: 225–443.
Buvat, R. 1952. Ann. Sc. Nat. **13**: 199–300.
Candolle, A. P. de. 1819. Théorie élémentaire de la botanique.
Dickson, J. 1936. Am. J. Bot. **23**: 385–393.
Douglas, G. 1936. Am. J. Bot. **23**: 199–212.
Eames, A. J. 1951. New Phytol. **50**: 17–35.
Eckhart, Th. 1954. Ber. D. Bot. Ges. **67**: 113–128.
———. 1955. Ber. D. Bot. Ges. **68**: 167–182.
Emberger, L. 1944. Les Plantes fossiles etc.
Fagerlind, F. 1958. Sv. Bot. Tidskr. **52**: 421.
Foster, A. S. 1936. Bot. Rev. **2**: 349–372.
Gregoire, V. 1938. La Cellule **47**: 287–452.
Hagerup, O. 1933. Kgl. Danske Vidensk. Selskab. Biol. Medd. **10**: 7.
———. 1938. Idem **14**: 1–34.
———. 1939. Idem. **15**: 1–39.
Joshi, A. C. 1947. Journ. Indian. Bot. Soc. **26**: 6–74.
Lam, H. J. 1947. Blumea. **6**: 282–289.
———. 1950. Sv. Bot. Tidsk. **44**: 517–534.
———. 1955. Acta Bot. Neerl. **4**: 410–428.
Leinfellner, W. 1950. Oest. Bot. Zeits. **67**: 403–435.
Lister, G. 1883. J. Linn. Soc. Bot. **20**: 423–429.
Matzke, E. B. 1932. Am. J. Bot. **19**: 477–507.
Payer, J. B. 1857. Traité d'organoginie comparée de la fleur (Paris).
Philipson, W. R. 1949. Biol. Rev. **24**: 21–50.
Puri, V. 1951. Bot. Rev. **17**: 251–353.
———. 1952. Idem. **18**: 603–651.
Schaefer, B. 1890. Flora. **73**: 62–104.
Sprotte, K. 1940. Bot. Arch. **40**: 463–506.
Tieghem, Ph. van. 1868. Ann. Sc. Nat. Bot. **5**, 12: 127–226.
———. 1875. Mem. Ac. Sc. Fr. **21**: 1–261.
———. 1881. Traité de Botanique.
Thomson, B. F. 1942. Am. J. Bot. **29**: 333–349.
Troll, W. 1939. Chronica botanica. **5**: 38–41.
Zimmermann, W. 1949. Geschichte der Pflanze.

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DIE VEGETATIONSKUNDLICHE STELLUNG VON CAREX BUXBAUMII WAHLENB. IN EUROPA, BESONDERS IN DEN NIEDERLANDEN

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Unter Mitwirkung von J. van Dijk *(Vereeniging tot Behoud van Natuurmonumenten (Naturschutzbund), Amsterdam)* [1]

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1. Pflanzengeographische und soziologische Verhältnisse im europäischen Areal der Art (Tabelle I)

Carex buxbaumii Wahlenb. ist eine amphi-atlantische boreale Art, beschrieben in 1803. Ihr Areal ist weniger genau bekannt als dasjenige der meisten europäischen *Carex*-Arten, indem A. Cajander erst in 1935 *C. hartmannii* von ihr abtrennte. Für die Diagnosen der beiden Arten sei u.A. auf Cajander (1935), Koch (1943) und Oberdorfer (1949) verwiesen. Das Areal von *Carex buxbaumii* s.s. ist u.A. von Kern & Reichgelt (1954) beschrieben und von Hultén (1950, 1958) dargestellt worden; Hultén (1950) bringt sie zu der Gruppe "boreal-circumpolar species that are boreal-montane in Europe but with gaps in Siberia", eine kleine Artengruppe, zu welcher u.A. auch *Listera cordata* gehört. Nach der Darstellung bei Hultén (1958) wäre das mehr oder weniger geschlossene Areal der Art beschränkt auf: Skandinavien (ausser SW-Norwegen); Finland (ausser W-Küste); Alpen (selten); Bayern, Ost-Deutschland, Polen und einen ziemlich schmalen O-W-verläufenden Streifen in Mittel-Russland. Weiterhin kommt *Carex buxbaumii* noch in isolierten, oft weit von einander entfernten Fundstellen vor in Schottland, Niederlande (sieh unten), West-Deutschland ausser Bayern (nur 2 Fundorte in Schleswig-

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[1] Die vorliegende Arbeit is eine gemeinschaftliche Veröffentlichung des Hugo de Vries-Laboratorium der Universität von Amsterdam, des Laboratorium für Pflanzensystematik und -Geografie der Landwirtschaftlichen Hochschule, Wageningen (Belmontia B. Ecology, fasc. 5), und des Reichsinstitutes für ökologische Grundlagenforschung des Naturschutzes, Bilthoven (R.I.V.O.N., Mitteilung Nr. 60). Sie ist ein Ergebnis von Gelände-Aufnahmen von J. van Dijk, W. J. Reijnders, S. Segal und V. Westhoff, bearbeitet von S. Segal und V. Westhoff. Die Aufnahmen des zweiten Verfassers datieren z.T. aus seiner Stelle am Laboratorium für Pflanzensystematik und -Geografie in Wageningen, z.T. aus seiner heutigen Stelle.

Holstein), Frankreich (sieh ENGEL 1953), SW-Norwegen, Balkan, dem asiatischen Teil der Sovjet-Union, Canada, den Vereinigten Staaten, Algier, Natal und Australien. Aber auch innerhalb des "geschlossenen Areals" ist die Art doch immerhin mehr oder weniger selten: so erscheint das "geschlossene Areal" in Skandinavien in der mehr kleinmassstäbigen Darstellung HULTÉNS (1950) sehr aufgelockert und ist es nach den Normen letzterer Arbeit nicht geschlossen.

Carex buxbaumii wurde in den Niederlanden zuerst beobachtet in 1898 von D. Lako und J. W. C. Goethart, im Land van Vollenhove (NW-Overijsel); sieh Flora Batava (1901) und VUYCK (1899). Schon in 1905 betonte GOETHART die Notwendigkeit des besonderen Schutzes dieser seltenen Art. VAN SOEST (1933) betrachtet die Art mit Recht als charakteristisch für das "Hafdistrict", d.h. das pflanzengeographische Distrikt der holozänen Meereston- und Niederungsmoorböden, jetzt hauptsächlich mit *Lolieto-Cynosureten* bewachsen, jedoch vegetationskundlich charakterisiert durch Gesellschaften der *Potametalia*, *Phragmitetalia* und *Caricetalia fuscae*. KERN & REICHGELT (1954) erwähnen als Fundstellen: drei in NW-Overijsel, näml. bei Wanneperveen, zwischen St. Jansklooster und De Belt, und zwischen Hasselt und Lichtmis; und eine bei Nieuwkoop in Südholland. Von diesen Lokalitäten sind diejenige bei Wanneperveen, zwischen Hasselt und Lichtmis und bei Nieuwkoop von uns im Gelände studiert worden; ausserdem wurde in N.W.-Overijsel von uns noch eine vierte Stelle beobachtet und aufgenommen und zwar am Kierse Wiede bei Meppel. Im Ausland sahen wir die Art nur im Ried d'Herbsheim, Elsass, Frankreich (1954). Von allen uns bekannten Fundorten ist die bei Wanneperveen bei weitem die meist ausgedehnte; die Art wächst hier optimal und z.T. gesellschaftsbildend, ihre ökologische Amplitude liess sich hier am besten studieren. Die Lokalitäten bei Wanneperveen, Meppel und Nieuwkoop sind geschützt: erstere sind Besitz der "Vereeniging tot Behoud van Natuurmonumenten in Nederland", die letztere ist Besitz der "Stichting het Zuidhollandsch Landschap". Eine Auswahl unseres Gesamtaufnahmenmaterials von *Carex buxbaumii* ist in Tabelle 2 dargestellt worden.

Bezüglich der Ökologie der Art schreibt HEGI (Fl. Mitt.): "zerstreut auf fruchtbaren, feuchten Wiesen, auf Riedwiesen (häufig auf Torf). Meist gesellig. Vorzügliche Streuepflanze". Die genauere und modernere Aussage von OBERDORFER (1949) stimmt damit wesentlich überein: "selten, aber gesellig in Kleinseggengesellschaften auf nährstoffreichen kalkfreien, wie kalkführenden Torfböden, in Verlandungsgesellschaften hinter dem Grossseggengürtel oder in Zwischenmooren mit *Carex lasiocarpa*, auch gesellschaftsbildend im *Eriophorion latifolii*-Verband (vgl. Kleinarten), reg. *Caricetea fuscae*-Art, gute Streupflanze".

In den älteren niederländischen Floren wurde der Standort angegeben als "vruchtbare weiden", wohl aus dem deutschen übersetzt. Nach der heutigen Lage trifft diese Erwähnung nicht zu, indem "vruchtbare weiden" jetzt aus *Lolieto-Cynosuretum* bestehen und die Art in dieser Assoziation überhaupt fehlt. Es soll aber nicht vergessen werden, dass das niederländische Grünland vor etwa fünfzig Jahren noch überwiegend aus Mager- und Streuwiesen bestand, und dasz innerhalb dieser Kategorie der Begriff "vruchtbare weiden" eine andere Bedeutung hatte. Dasjenige, dasz damals "vruchtbaar" hiess, würde nach den heutigen agrarischen Normen als arm und improduktiv bezeichnet werden. Derartige unbestimmte, relative ökologische Angaben, wie man sie leider noch in den meisten Floren findet, sind für geobotanische Deutung ohne weiteres ungeeignet. KERN & REICHGELT (1954) geben an: "in blauwgrasland op vochtige, schrale veenen zandgrond", d.h. in Streuwiesen auf wechselfeuchten, mageren Torf- und Sandböden. Wir werden weiterhin aber sehen, dasz *Carex buxbaumii* in den Niederländen innerhalb dieses ökologischen Rahmens einen gewissen Nährstoffreichtum tatsächlich nicht scheut.

Carex buxbaumii steht also nach OBERDORFER (l.c.) in Süd-deutschland auf kalkfreien wie kalkführenden Torfböden und tritt nach unserer Beobachtung im Elsass auf kalkreichem Sumpf vegetationsbildend auf; jedoch wurde sie in den Niederlanden nur auf kalkfreier Unterlage beobachtet. Man wäre vielleicht geneigt, diese Erscheinung zu betrachten als ein Beispiel der Erfahrungstatsache, dasz gewisse Arten in Mitteleuropa mehr oder weniger calcicol bzw. neutrophil auftreten, dagegen im atlantischen Bereich kalkfreien und saueren Standorten bevorzügen oder gerade darauf beschränkt sind. Ohne in dieser Frage jetzt zu entscheiden, sei zuerst darauf hingewiesen, dasz *Carex buxbaumii* nach CAJANDER (1935) in Fennoskandien als mehr oder weniger kalkhold erscheint, obwohl sie da öfters auch auf kalkfreien Böden auftritt. CAJANDER vermutet, dasz Kalkgehalt des Bodens die Konkurrenzkraft der Art steigert.

Um die Frage des eventuellen unterschiedlichen ökologischen Verhalten der *Carex buxbaumii* in verschiedenen Teilen Europas genauer beurteilen zu können, haben wir einige Vegetationstabellen, in welchen die Art auftritt, in unserer Tabelle 1 zusammengefasst. Diese Tabelle enthält Material aus Süddeutschland (OBERDORFER 1957), französischem Elsass (ISSLER 1932), Polen (ZARZYCKI 1958), Schweden (ALMQUIST 1929) und den Niederlanden (unserer Tabelle II entnommen).

Jede Assoziation stellt ein Gefüge verschiedener ökologischen Artengruppen da; dieses Gefüge lässt sich lokal analysieren indem man die Artenliste in Gruppen ökologischer Differentialarten aufteilt. Für regionalen Vergleich reicht diese Methode aber nicht aus. Es ist dazu vielmehr notwendig, die Artengruppen in Termen des pflanzensoziologischen Systems auszudrücken. Freilich soll mann dann aber nicht — wie es leider öfters geschieht — so vorgehen, dasz man nur die hierarchische Reihe der Assoziations-, Verbands-, Ordnungs- und Klassenkennarten desjenigen Verbandes (usw.) unterscheidet, zu welchem man die Assoziation stellt, und sonstige Arten als "Begleiter" darstellt. Auf diese Weise entstehen schöne Tabellen, die aber über das wirkliche ökologische Gefüge wenig aussagen. Für ausreichende Information braucht man eine gleichwertige Berücksichtigung der Kennarten anderer Verbände, Ordnungen und Klassen, insoweit diese in der Tabelle vertreten sind, und, wenn nicht in solchen Kategorien auszudrücken, Gruppen ökologischer Zeigerarten; die Gruppe der "sonstigen Arten" soll minimal bleiben.

In manchen Fällen bietet dieses Vorgehen aber die Schwierigkeit, dasz die Zugehörigkeit der Arten zu den Einheiten des pflanzensoziologischen Systems keineswegs feststeht. Es gibt da zwischen den Autoren verschiedener Gebiete beträchtliche Auffassungsunterschiede. Dies ist besonders der Fall bei der hier betrachteten Vegetationsgruppe der "*Molinieto-Arrhenatheretea*" und "*Scheuchzerio-Caricetea fuscae*". Die zweite Klasse wird allerdings von allen Autoren anerkannt; bezüglich der ersten gehen die Meinungen aber schon auseinander. Indem die mitteleuropäischen Autoren sie meistens anerkennen, besteht im atlantischen Nordwesteuropa die Auffassung, dasz entweder die *Molinietalia* zu den *Scheuchzerio-Caricetea* zu stellen sind und die *Arrhenatheretea* eine Klasse für sich bilden (VLIEGER 1937, WESTHOFF 1947) oder dasz die *Molinietalia* zur Klasse *Molinio-Juncetea* zu stellen sind, indem die *Arrhenatheretalia* ebenfalls eine Klasse für sich bilden (LEBRUN c.s. 1949). Es liegt dieser Differenz wohl mit zum Grunde, dasz die atlantischen wechselfeuchten Magerwiesen wesentlich reicher an acido- und hygrophilen Arten sind als die mitteleuropäischen und dagegen wesentlich ärmer an Kalk- und Nährstoffzeiger. Selbstverständlich gibt es auch bei Betrachtung der Zugehörigkeit der Arten innerhalb der Klassen mehrere Auffassungsdifferenzen.

Es kann nicht die Aufgabe der vorliegenden Arbeit sein, derartige Fragen, wenn auch nur vorläufig, lösen zu wollen; dazu sind Übersichtstabellen eines grossen geographischen Raumes unbedingt notwendig. Um Einheitlichkeit der Einteilung zu erreichen und daher regionalen Vergleich zu ermöglichen, haben wir unsere Einteilung daher im grossen Ganzen gestützt auf derjenigen OBERDORFER's (1957), der am meisten ausgearbeiteten und meist rezenten Vegetationsmonographie eines grösseren Raumes. OBERDORFER stellt die *Molinietalia* zu den *Molinieto-Arrhenatheretea.* Um eine diesbezügliche Entscheidung zu vermeiden, haben wir in unseren Tabellen die Verbandskennarten und die Ordnungskennarten des *Molinion* und der *Molinietalia* gesondert aufgeführt, sowie auch die Gesamtartengruppe der *Scheuchzerio-Caricetea fuscae*, die Gruppe der gemeinschaftlichen Arten der *Molinietalia* und *Scheuchzerio-Caricetea*, und die Gruppe der gemeinschaftlichen Arten der *Molinietalia* und *Arrhenatheretalia* (also die sog. Klassenkennarten der *Molinieto-Arrhenatheretea).* Eine kleine, aber interessante Gruppe wird weiterhin gebildet von denjenigen Arten, welche den *Molinietalia*, den *Scheuchzerio-Caricetea fuscae* und den *Brometalia erecti* gemeinschaftlich sind. Ausserdem sind gesondert aufgeführt: die Verbandskennarten des *Calthion* und des *Filipendulo-Petasition*, also der zu den *Molinietalia* zu stellen staunassen bis wechselfeuchten Streuwiesen und Hochstaudenfluren auf etwas nährstoffreicheren Böden; die Verbands- und Ordnungskennarten der *Arrhenatheretalia*, also der Wiesen auf nährstoffreichen wechselfeuchten Böden; die Gruppe der Arten welche *Calthion*, *Filipendulo-Petasition* und *Senecion fluviatilis* gemeinschaftlich sind, d.h. Arten der Hochstaudenfluren auf nitratreicherem Boden; die Verbands- und Ordnungskennarten der *Nardetalia*, d.h. Zeigerarten der nach Heiden übergehenden mageren Triften auf trocken-wechselfeuchten, nährstoffarmen Böden; die Verbands-Kennarten des *Agropyro-Rumicion crispi*, also Zeigerarten von Kriechrasen auf nährstoffreichen, feuchten, ruderalen oder aus natürlichen Ursachen nitratführenden Böden; die Verbands-kennarten des *Magnocaricion* und Ordnungs-kennarten der *Phragmitetalia*, also Arten aus den syndynamisch vorhergehenden Verlandungsgesellschaften des Grossseggengürtels in ± nährstoffreichem Wasser; die Verbands- und Ordnungs-kennarten der *Brometalia erecti*, also der Kalktrockenrasen; die Arten der oligo-dystrophen Hochmoorgesellschaften der *Oxycocco-Sphagnetea;* die Differentialarten der *Molinietalia* gegenüber den *Arrhenatheretalia;* und die Gruppe derjenigen Feuchtigkeitszeiger, welche zu bewerten sind als Differentialarten der Gesellschaften die "feuchter" sind als die *Molinietalia.*

Freilich schliessen einige dieser Gruppen einander aus: *Brometalia*-Arten und *Oxycocco-Sphagnetea*-Arten wächsen nicht in demselben Bestand (vergl. Spalten 1 und 5–6 der Tabelle I). *Brometalia*- und *Phragmitetalia*-Arten, obwohl in ihrem ökologischen Benehmen auch grundverschieden, haben allerdings die Nährstoffreichtum des Standortes gemein; sie können daher zusammen auftreten und deuten dann auf sehr stark wechselfeuchtem Boden (Tabelle I, Spalte 1).

Obwohl eine Unterverteilung der Artengruppe der *Scheuchzerio-Caricetea fuscae* auch angebracht wäre, ist davon aus Grunden der Übersichtlichkeit abgesehen worden, weil die hier studierte Gesellschaften sehr artenreich sind und z.B. in den Niederlanden mit bis 90 Arten auf 100 m² Fläche zu den artenreichsten des Landes gehören.

Nur eine derartige Untergliederung ermöglicht einen fruchtbaren ökologischen Vergleich zwischen Gesellschaften weit auseinanderliegenden Gebiete mit Bezug auf der ökologischen Amplitudo einer gewissen Art.

Aus der Tabelle I geht zuerst hervor, dasz das süddeutsche "*Cnidio-Juncetum*" von OBERDORFER (1957) und das polnische "*Molinietum typicum*" von ZARZYCKI (1958) ziemlich stark übereinstimmen. Beide Assoziationen sind, wohl mit Recht, von ihren Autoren zum *Molinion*-Verbande gestellt. OBERDORFER nennt das *Cnidio-Juncetum* eine Lokalassoziation der nördlichen Rheinebene, die als kalkarme Parallelform des *Molinietum medioeuropaeum* bzw. östlicher *Cnidium*-reicher *Molinieten* aufgefasst werden kann und in ähnlicher Form neuerdings auch im Elsass nachgewiesen sei (sehe aber unten). Aus den von ZARZYCKI (1958) erwähnten pH-Werten des Bodens (H_2O: 5,2–6,73; KCl: 4,3–5,92) ist zu schliessen, dasz der Boden seines *Molinietums*, wie auch derjenige des *Cnidio-Juncetums* Oberdorfers, relativ nährstoffreich ist, jedenfalls nach atlantischen Massstäben. Beide Assoziationen, die westdeutsche und die polnische, wächsen auf stark wechselfeuchten Böden. Beide zeigen sowohl *Brometalia*-Arten wie Feuchtigkeitszeiger; *J*edoch fehlen bei OBERDORFER die Arten der *Scheuchzerio-Caricetea juscae* und sind dagegen die *Brometalia* stärker vertreten, nach dem zu schliessen wäre, dasz der westdeutsche Standort trockener sei. Beide zeigen eine ganze Reihe *Arrhenatheretalia*-Arten (Nährstoffreichtum!), viel mehr als in den anderen in der Tabelle I vereinigten Gesellschaften. Beide weisen aber auch eine beträchtliche Gruppe *Nardetalia*-Arten auf (Magertriftenzeiger!). *Carex buxbaumii* erscheint bei OBERDORFER als Differentialart der Assoziation mit Präsenz III (Abundanz und Dominanz nicht erwähnt); bei ZARZYCKI als Begleiter mit Abundanz + bis 1. Letztere Abundanz ist, in Vergleich zu den Verhältnissen bei ISSLER (1932) und in den Niederlanden, nicht optimal.

Im ersten Blick erscheinen die Verhältnisse in der Arbeit von ISSLER (1932) aus dem französischen Elsass wesentlich verschieden. Die *Brometalia*-Arten und die andere Trockenheitszeiger fehlen ganz, sowie die Arten, die den *Molinietalia*, den *Scheuchzerio-Caricetea* und den *Brometalia* gemein sind. Auch die *Arrhenatheretalia*-Arten und die sog. Klassenkennarten der *Molinieto-Arrhenatheretea*, sowie die *Nardetalia*-Arten sind aber überhaupt nicht da, und die *Molinietalia*-Arten sind nur schwach vetreten. Der Standort ist wesentlich feuchter (sieh *Carex hudsonii*, *Iris pseudacorus*, *Juncus subnodulosus);* eben *Molinia coerulea* spielt nur eine ganz untergeordnete Rolle. ISSLER (l.c.) stellt diese von ihm "*Buxbaumietum*" genannte Assoziation denn auch zum *Magnocaricion elatae* (ob mit Recht, sei dahingestellt), und beschreibt sie syndynamisch als eine Verlandungsgesellschaft in der Sukzession zwischen dem "*Strictetum*" (= *Carex hudsonii*-Gesellschaft) und dem "*Hornschuchietum*" (= *Carex hostiana*-Gesellschaft), indem sie auch in Kontakt treten mag mit dem feuchten *Juncetum obtusiflori* und dem *Cladietum marisci*. In dieser Gesellschaft bildet *Carex buxbaumii* ausgedehnte Bestände mit Dominanz 5 und Soziabilität 5 in den vier von ISSLER gegebenen Aufnahmen; die Art ist hier also zweifellos optimal, weit mehr als in den vorher erwähnten süddeutschen und polnischen Assoziationen. Jedoch stimmt der von ISSLER beschriebene Standort mit dem von OBERDORFER und ZARZYCKI beschriebenen überein in ihrem Nährstoffreichtum. Letzterer erklärt wahrscheinlich auch die auffällige Armut an Arten der *Scheuchzerio-Caricetea fuscae*, trotz des nassen Standortes. In dieser Beziehung unterscheiden die *Carex buxbaumii*-Bestände aus dem Elsass sich wesentlich von den niederländischen und schwedischen.

Während einer internationalen Grünlandexkursion (Association internationale de phytosociologie, 1954) hat der zweite Verfasser versucht, die von Issler beschriebenen Bestände wiederzufinden. Es ist ihm leider nicht gelungen, z.T. weil der Grundwasserstand dieses ganzen Gebietes in den letzten Jahrzehnten erheblich gesenkt ist (bedingt durch Meliorationsmassnahmen am Rhein). Die einzige Aufnahme eines *Carex buxbaumii*-Bestandes im Elsass, die damals gemacht werden könnte, findet sich in Tabelle II: sie zeigt einen wesentlich weniger feuchten Standort als der von ISSLER beschriebene.

Noch einige Worte über dem Folgestadium des Isslerschen *Buxbaumietum*, der "Association à *Carex hornschuchiana*" (= *C. hostiana).* Nach ISSLER bildet diese Gesellschaft in der Sukzession ein Bindeglied zwischen dem "*Strictetum*" (oder auch dem "*Buxbaumietum*"*)* und dem *Molinietum*. Ohne daran zweifeln zu wollen, sei dennoch bemerkt, dasz die "Association à *Carex hornschuchiana*" nach der von ISSLER gegebenen Tabelle unbedingt zum *Molinietum* zu stellen sei. ISSLER (l.c.) bemerkt, dasz *Carex hostiana* von schweizerischen und französischen Autoren als Kennart der *Scheuchzerio-Caricetea fuscae* betrachtet wird (vergl. die von ihm zitierte Litt.) und er ist damit einverstanden; er weist aber darauf hin, dasz *Carex hostiana*, von ihm eine sarmatische Art genannt, nach dem N.W. Europas ausklingt und dasz sich dort anscheinend auch ihre ökologische Amplitudo verschmälert. Auch jetzt wird *Carex hostiana* in Mitteleuropa noch als Art der *Scheuchzerio-Caricetea fuscae* und zwar als *Eriophorion latifolii*-Verbandskennart gewertet (OBERDORFER 1949, 1957). Es ist daher von Bedeutung, zu bemerken, dasz diese Art in dem niederländischen *Molinietum* nicht nur häufig und hochpresent auftritt, sondern da auch als exklusive Assoziations-kennart gilten kann; dieses niederländische *Molinietum* ist (nach der atlantischen Kennart *Cirsium dissectum)* als *Cirsieto-Molinietum* beschrieben worden (vergl. z.B. WESTHOFF, DIJK, PASSCHIER u. SISSINGH 1946). Dasz diese Assoziation und damit auch *Carex hostiana* jetzt in den Niederlanden äusserst selten geworden sind, ist nur von agrikultur-technischen Massnahmen bedingt. Die Frage, inwieweit aus diesem und derartigen Gründen das *Cirsieto-Molinietum* vielleicht gar nicht zum *Molinion*, sondern vielmehr zum *Eriophorion latifolii*-Verband zu stellen wäre (PREISSING, mündl.) ist auch für unsere weiteren Betrachtungen wichtig, kann aber in diesem Rahmen nicht weiter verfolgt werden.

Wir kommen jetzt zum soziologischen Verhalten von *Carex buxbaumii* in den Niederlanden: Tabelle I, Spalten 5 und 6. Diese Gesellschaft gehört derselben Feuchtigkeitsstufe an wie die von ISSLER beschriebene. Auch hier fehlen die *Brometalia*-Arten und sonstige Trockenheitszeiger ganz; die *Phragmitetalia*-Arten und sonstige Feuchtigkeitszeiger sind eben noch stärker vertreten. Die Zahl der *Molinietalia*-Arten ist jedoch beträchtlich höher. Vor allem springt aber das starke Anschwellen der Artengruppe der *Scheuchzerio-Caricetea fuscae* ins Auge. Zumal in N.W.-Overijsel ist diese Gruppe mit 23 Arten derjenigen der *Molinietalia* (10 Arten) weit überlegen; zählt mann zu den *Molinietalia*-Arten auch die Artengruppen des *Calthion*, *Filipendulo-Petasition* und *Senecion fluviatilis*, dann halten beide einander die Waage. Die Gruppe der gemeinschaftlichen Arten der *Molinietalia* und *Arrhenatheretalia* ("*Molinieto-Arrhenatheretea*-Arten") wird aber von der Gruppe der gemeinschaftlichen Arten der *Molinietalia* und *Scheuchzerio-Caricetea fuscae* eindeutig übertroffen (8 gegen 14). Selbstverständlich sollen nicht nur die Artenzahl, sondern auch die Präsenz und Dominanz berücksichtigt werden; aus der Tabelle geht aber hervor, dasz unsere Folgerungen dadurch nicht beeinträchtigt werden.

Die in den Spalten 5 und 6 der Tabelle I dargestellte Gesellschaft weicht aber vom typischen niederländischen *Cirsieto-Molinietum* beträchtlich ab. In letzterem sind die *Scheuchzerio-Caricetea-fuscae*-Arten viel schwächer, die *Molinietalia*-Arten viel stärker vertreten. Es darf aus dieser Tabelle denn auch keineswegs der Schluss gezogen werden, dasz das typische *Cirsieto-Molinietum* nicht zum *Molinion*-Verband gehöre. Die Tabelle sagt nur aus, dasz *Carex buxbaumii* in den Niederlanden charakteristisch ist für eine Übergangsgesellschaft zwischen *Scheuchzerio-Caricetea fuscae* und *Molinietalia.* Wir haben diese Übergangsgesellschaft aus Zweckmässigkeitsgründen noch zum *Cirsieto-Molinietum* gestellt und als "Subassoziation mit *Carex buxbaumii*" unterschieden. Differentialarten dieser Subassoziation sind somit, ausser *Carex buxbaumii*, die syndynamischen Zeigerarten der *Scheuchzerio-Caricetea fuscae*, vor allen *Carex diandra*, *Carex lasiocarpa*, *Comarum palustre*, *Stellaria palustris*, *Juncus subnodulosus*, *Carex curta*, *Menyanthes trifoliata*, *Epilobium palustre;* diese treten im *Cirsieto-Molinietum typicum* nur ausnahmsweise und vereinzelt auf. Dasselbe gilt jedoch nicht für *Carex hostiana* (sehe oben) und *Carex pulicaris*, welche als Kennarten des *Cirsieto-Molinietum* zu betrachten sind.

Ein auffälliger Merkmal des *Cirsieto-Molinietum caricetosum buxbaumii* ist, verglichen mit den in den Spalten 1, 2 und 3 der Tabelle I wiedergegebenen Gesellschaften, das Ansteigen der Artengruppe des *Calthion* und des *Filipendulo-Petasition.* Zum Teil erklärt sich diese Erscheinung dadurch, dasz *Carex buxbaumii* auf relativ schmalen Übergangsstreifen zwischen Schwingrasen *(Caricetum diandrae)* und Streumagerwiesen *(Cirsieto-Molinietum typicum)* wächst und dort in Kontakt steht mit den Hochstaudenfluren des *Valerianeto-Filipenduletum.*

Das niederländische *Cirsieto-Molinietum caricetosum buxbaumii* zeigt aber auch eine gewisse Übereinstimmung mit den süddeutschen und polnischen Gesellschaften und einen Unterschied mit der von ISSLER beschriebenen Assoziation, nämlich im Auftreten der Gruppe der *Nardetalia*-Arten und der Gruppe der gemeinschaftlichen Arten der *Molinietalia*, *Scheuchzerio-Caricetea fuscae* und *Brometalia.* Dieses Merkmal deutet auf einem gewissen Magerrassencharakter mit zeitweiliger Austrocknung, dasz den elsässischen eutrophen Verlandungsbeständen fremd ist.

Es sei weiter darauf hingewiesen, dasz die Gruppen der *Arrhenatheretalia*-Arten und der *Agropyro-Rumicion crispi*-Arten, wenn auch schwach, in der niederländischen *Carex buxbaumii*-Gesellschaft vertreten sind. In *Cirsieto-Molinietum typicum* fehlen diese Arten völlig; sie wären da nur als Störung zu betrachten. *Carex buxbaumii* scheint sich an diesen etwas nährstoffreicheren Stellen aber eher besser zu entwickeln (vergl. oben, zumal den Ausführungen CAJANDERS).

Der grösste Unterschied zwischen dem *Cirsieto-Molinietum caricetosum buxbaumii* und die erwähnten *Carex buxbaumii*-Gesellschaften aus südlicheren Gegenden liegt aber vielleicht im Auftreten der Hochmoor-Artengruppe der *Oxycocco-Sphagnetea*, zusammen mit dem häufigen Vorkommen von nicht zu dieser Klasse zu stellen *Sphagnum*-Arten *(S. palustre, S. recurvum, S. fimbriatum, S. squarrosum)*. In diesem Merkmal leitet die niederländische Gesellschaft zu den schwedischen über, welche wir jetzt besprechen werden.

In dem von Almquist (1929) aus Uppland beschriebenen "*Carex hornschuchiana-Amblystegium*-Kärrang" sind die *Molinietalia*-Arten nur schwach und dagegen die *Scheuchzerio-Caricetea fuscae*-Arten sehr stark vertreten. Die Gesellschaft gehört zweifellos zu der letzten Klasse.

TABELLE I

Einige Daten über das soziologische Verhalten von Carex buxbaumii in Europa.
Regionale Präsenztabelle.

Erläuterung:

D: Süddeutschland
F: Frankreich (Rheinebene)
P: Polen (Oberer Weichseltal)
S: Schweden (Uppland)
N I: Niederlande (Nieuwkoop: Zentrum des Landes)
N II: Niederlande (Wanneperveen: Nordwest-Overijsel)
Ob: Oberdorfer
Iss: Issler
Zar: Zarzycki
Alm: Almquist
div: Verfasser und Mitarbeiter

C.-J.: Cnidio-Juncetum
Bx: Buxbaumietum
Mt: Molinietum typicum
C.A.K.: Carex hornschuchiana-Amblystegium-kärräng
C.-M.c.b.: Cirsieto-Molinietum, Subass. von Carex buxbaumii
Mo: Molinion coeruleae
MC: Magnocaricion elatae
C.l.: Caricion lasiocarpae
Cl/Mo: Übergang zwischen Caricion lasiocarp und Molinion coeruleae

In jeder Spalte sind zuerst die Präsenz, nach dieser die höchste und die niedrigste Abundan Dominanzzahl aufgeführt. Letztere Werte entsprechen in den Spalten 1–3 u. 5–6 die Skala v Braun-Blanquet, jedoch in der Spalte 4 die Skala von Hult-Sernander. Bei Oberdorfer (Spalte finden sich die Abundanz–Dominanzverhältnisse nicht erwähnt.

Mit ( ) sind aufgeführt diejenigen Arten, die zwar in den hier berücksichtigten Aufnahm fehlen, jedoch bei den betreffenden Autoren in anderen Untereinheiten ihrer Tabelle erwähnt sin

	1	2	3	4	5	6
Land	D	F	P	S	N I	N II
Autor	Ob.	Iss.	Zar.	Alm.	div.	div.
Jahr d. Veröff.	1957	1932	1958	1929	1959	1959
Zahl der Aufnahmen	7	4	4	9	4	6
Namen der Gesellschaft (von den betreff. Autoren geg.)	C.-J.	Bx.	Mt.	C.A.K.	C.-M.c.b.	C.-M.c.
Verband	Mo.	MC	Mo.	C.l.	Cl/Mo	Cl/Mo
Carex buxbaumii	III	4. 5.	2.+–1	II. 1–2	4 2–3	V 2
(angeführt als):	D. Ass.	Char. (Dom.)	Begl.	—	D. Subass.	D. Sub ass.
Kennarten der Assoziationen:						
Cnidium dubium	III	—	1.+	—	—	—
Viola stagnina	I	—	—	—	—	II.1
Viola pumila	II	—	—	—	—	—
Oenanthe peucedanifolia	I	—	—	—	—	—
Iris sibirica	—	—	2.+	—	—	—
Laserpitium prutenicum	—	—	1.3	—	—	—
Cirsium dissectum	—	—	—	—	—	II.1
Cirsium spurium	—	—	—	—	—	I.+
Viola ritschliana	—	—	—	—	—	I.+
Verbands-Kennarten Molinion:						
Succisa pratensis	V	—	3.1–3	III.1	2.2	III.+–
Thalictrum flavum	III	—	—	I.+	III.+	II.+
Serratula tinctoria	(I)	1 +	4 +–2	—	—	—
Selinum carvifolia	III	—	4 +–1	—	—	—
Gentiana pneumonanthe [1]	III	—	4 +	—	—	—
Galium boreale	IV	—	3 +–2	—	—	—
Allium angulosum	I	1 +	—	—	—	—
Cirsium tuberosum	IV	—	—	—	—	—

	1	2	3	4	5	6
ula salicina	III	—	—	—	—	—
anthus superbus	II					
hioglossum vulgatum	I	—	—	—	—	—
rex tomentosa	I	—	( )	—	—	—
chis coriophora	I	—	—	—	—	—
dnungs-Kennarten Molinietalia:						
thrum salicaria	III	1.1	1 +	I +	3 + 1	V +-1
nguisorba officinalis	V	1.+	4.2–3	—	—	V + 3
chnis flos-cuculi	III	—	2 +	—	3 + 1	IV +–1
tus uliginosus	III	—	1 +	—	4 +–1	III +
zula multiflora	III		1 +	—	4 + 1	IV +
ncus conglomeratus	III	—	4 +–2	—	1 +	IV +
inanthus glaber	—	—	3 + -1	—	3 +	II + -1
hillea ptarmica	V	—	—	—	1.1	IV +
uisetum palustre	III	—	4 +–1	II 1	—	—
rsium palustre	II	—	—	—	4 +–1	V + 1
aum silaus 1)	IV	—	2 +	—	—	—
tonica officinalis	IV	—	4 +–2	—	—	—
ncus acutiflorus	V	—	—	—	—	I +
nunculus polyanthemus . . .	—	—	2 +–1	—	—	—
pericum maculatum	II	—	—	—	—	—
lygala amara	II	—	—	—	—	—
rbands-, Ordn.- u. Klassen-Kennarten Scheuchzerio-Caricetea fuscae:						
rex hostiana	—	4.1	4.1-2	V 1 4	( )	(I +)
ncus subnodulosus	—	1.1	—	II 1	3 +–2	I 2
rex lasiocarpa	—	1 +	—	III 1–2	—	III 1–2
rex nigra	—	—	4 +–1	I +	—	I 1
mpylium stellatum	—	—	1 +	IV +–5	—	I 1
dicularis palustris	—	—	( )	I 1	3 + -1	II +–1
marum palustre	—	—	—	II 1	3 + 2	V +–2
ola palustris	—	—	—	—	1 +	IV +–1
rex davalliana		+.1	I +	—	—	—
enyanthes trifoliata	—	—	( )	III 1–2	—	IV 2–3
ilobium palustre	—	—	—	—	1 +	II +
paris loeselii	—	—	—	—	1 +	I +
gina nodosa	—	—	—	—	2 +	I +
orpidium scorpidioides	—	—	—	II +–1	—	I +
epanocladus intermedius . . .	—	—	—	V + 5	—	I 2
chis palustris	—	1 +	—	—	—	—
rex flava (s.s. = C. eu-flava) .	—	—	—	I +	—	—
rex diandra	—	—	—	—	—	IV + 3
rex pulicaris	—	—	—	—	—	III + -1
rex curta	—	—	—	—	—	III +
rex dioica	—	—	—	IV 1–4	—	—
llaria palustris	—	—	—	—	—	III +
iophorum gracile	—	—	—	—	—	I +
earchois pauciflora	—	—	—	II 1	—	—
iophorum latifolium	—	—	—	III +–1	—	—
yum pseudotriquetrum	—	—	( )	—	—	III +–1
ccardia pinguis	—	—	—	—	—	I 1
ccardia multifida	—	—	—	—	—	I +
mptothecium trichodes	—	—	—	I 2	—	—
iophorum angustifolium . . .	—	—	( )	II 1	—	( )

	1	2	3	4	5	6
Gemeinschaftliche Arten Molinietalia u. Scheuchzerio–Caricetea fuscae:						
Juncus articulatus	—	2 1	4 +–1	I +	1 +	I +
Galium uliginosum	II	—	4 +–2	I +	4 +–2	V +–
Salix repens	III	—	—	II 1	2 +	III +–
Hydrocotyle vulgaris	I	2 +–1	—	—	2 +–1	IV 1–2
Agrostis canina	III	—	( )	I 2	1 1	V 1–2
Dactylorchis incarnata	II	—	—	III 1	—	III +–
Dicranum bonjeani	—	—	—	—	2 2	I 2
Valeriana dioica	—	—	—	—	4 1–2	V +–
Parnassia palustris	—	—	—	I +	—	II 1
Ranunculus flammula	—	—	2 +–1	—	( )	( )
Carex demissa	—	—	—	—	2 +–1	II +
Hierochloe odorata	—	—	—	—	3 +–1	II +–
Mentha aquatica	—	—	—	—	3 +	IV 1
Epipactis palustris	—	—	2 1	I 1	—	—
Calamagrostis neglecta	—	—	—	—	—	V +–
Taraxacum (cf.) palustre	I	—	—	—	—	—
Pinguicula vulgaris	—	—	—	I 1	—	—
Gemeinsch. Arten Molinietalia, Scheuchzerio-Caricetea fuscae u. Brometalia:						
Briza media	III	—	4 +	I 1	—	I +
Leontodon nudicaulis	—	—	—	—	1 1	—
Linum catharticum	—	—	4 +–1	—	—	II +
Fissidens adiantoides	—	—	3 +	II +–1	—	III +–
Gymnadenia conopsea	II	—	—	—	—	—
Carex flacca	II	—	—	—	—	—
Calamagrostis epigeios	II	—	—	—	—	—
Differentialarten Molinietalia geg. Arrhenatheretalia:						
Molinia coerulea [1])	V 1–4	1 +	4 2–4	IV 1–4	4 +–2	V +–
Carex panicea	II	4 +–1	4 1–2	V 1–3	2 +	V +–
Galium palustre	II	2 +	( )	I 1	3 +	V +
Peucedanum palustre	—	2 +	—	II 1	4 +	V +–
Lysimachia vulgaris	V	—	1 1	—	3 +	III +–
Deschampsia caespitosa	V	1 +	3 +–2	—	—	—
Carex pallescens	I	—	2 +–2	—	—	—
Juncus effusus	I	—	—	—	1 1	( )
Symphytum officinale	III	—	—	—	—	I +
Chiloscyphus polyanthus	—	—	—	—	1 +	I +
Dactylorchis "latifolia"	—	—	3 +–1	—	—	—
Mnium punctatum	—	—	—	II 1	—	—
Stachys palustris	—	—	—	—	—	—
Sphagnum recurvum	—	—	—	—	—	II 4
Pellia epiphylla	—	—	—	—	—	III +–
Verbandskennarten Calthion u. Filip.-Petasition:						
Lathyrus paluster	I	3 +–1	—	II 1	2 +–2	IV +
Filipendula ulmaria	I	—	—	III 1	3 +–1	IV +–
Carex disticha	I	1 +	—	—	—	III +–
Angelica sylvestris	I	—	—	—	4 +	II +
Caltha palustris	—	1 1	( )	I +	( )	II +
Valeriana officinalis	—	—	—	—	3 +–2	V +

	1	2	3	4	5	6
necio aquaticus	I	—	—	—	—	I +
actylorchis praetermissa	—	—	—	—	3 +	II +
actylorchis praetermissa ssp. junialis	—	—	—	—	2 +	II +
rsium rivulare	—	—	2 +–1	—	—	—
anunculus auricomus (ssp.)	—	—	1 +	—	—	—
actylorchis majalis	—	—	—	—	1 +	—
ypericum tetrapterum	—	—	—	—	2 +	( )
meinsch. Arten Filip.-Petasition u. Senecion fluviatilis:						
ıpatorium cannabinum	—	—	—	—	4 +	IV +
alystegia sepium	—	—	—	—	3 +	( )
necio paludosus	—	3 +–1	—	—	—	—
ıphorbia palustris	—	1 +	—	—	—	—
rb.- u. Ordn.-Kennarten Arrhenatheretalia:						
icia cracca	III	—	1 +	I +	2 +	—
rifolium repens	I	—	3 +	—	—	I +
ynosurus cristatus	II	—	3 +–2	—	—	I +
stuca pratensis	III	—	4 +–1	—	—	—
rifolium pratense	III	—	4 +–2	—	—	—
hrysanthemum leucanthemum	IV	—	4 +–2	—	—	—
athyrus pratensis	I	—	2 +	—	—	—
alium mollugo	I	—	—	—	—	I +
ysimachia nummularia	II	—	1 +	—	—	—
hleum pratense	—	—	1 +	—	—	—
rifolium dubium	—	—	2 +–2	—	—	—
ampanula patula	—	—	1 +	—	—	—
ellaria graminea	—	—	1 +	—	—	—
uphrasia rostkoviana	—	—	3 +	—	—	—
emeinsch. Arten Molinietalia u. Arrhenatheretalia (sog. Klassenkennarten d. Molin.-Arrhenatheretea):						
olcus lanatus	V	—	4 +–2	—	3 +–1	V +–1
runella vulgaris	III	—	4 +–2	—	3 +	III +
umex acetosa	II	—	2 +	—	1 2	I +
anunculus acer	III	—	4 +–2	—	—	III +–1
lantago lanceolata	III	—	4 1	—	—	IV +–3
ardamine pratensis	I	—	2 +–1	—	—	IV +
limacium dendroides	III	—	2–3	—	—	II +–3
hinanthus minor	IV	—	1 +	—	—	—
entaurea jacea	IV	—	4 +–2	—	—	—
erastium holosteoides	I	—	2 +	—	—	—
hytidiadelphus squarrosus	—	—	—	—	—	IV +–3
erbands- u. Ordn.-Kennarten Nardetalia:						
otentilla erecta	V	—	4 +–2	III 1–2	4 +–2	III +–1
ieglingia decumbens	II	—	4 1–2	—	—	I +–1
olygala vulgaris	II	—	3 +–1	—	—	I +
estuca ovina	I	—	3 +	—	—	—
enista tinctoria	III	—	—	—	—	—
oeloglossum viride	I	—	—	—	—	—
alium pumilum	I	—	—	—	—	—

	1	2	3	4	5	6
Genista sagittalis	I	—	—	—		—
Nardus stricta	—		3 1–2			—
Viola canina	—		—			I +–
Potentilla anglica	—		—	—		I +
Dactylorchis maculata	I		—	—		—
Platanthera bifolia	—		I 1	—		—
Scorzonera humilis	—		I 1	—		—
Verbands-Kennarten Agropyro–Rumicion crispi:						
Ranunculus repens	III	2 1–2	1 1	—		I +
Festuca arundinacea	II	—	—	—		—
Gratiola officinalis	I	—	—	—	—	—
Potentilla reptans	I	—	—	—	—	—
Veronica scutellata	I					—
Verb.-K.A. Magnocaricion u. Ordn.-K.A. Phragmitetalia:						
Phragmites communis	III	1 1	3 +–2	III 1–2	4 1–2	V +–
Equisetum fluviatile	—	—	—	I 1	2 +–1	V +–
Carex acuta	III	—	—	—	—	III +–
Carex hudsonii	—	4 +	—	—	—	III +–
Carex acutiformis	—	1 +	—		1 +	—
Myosotis scorpioides	II	—	1 1			—
Carex riparia	—	1 +	—	—	—	—
Poa palustris	III	—	—	—	—	—
Typha angustifolia	—				1 +	—
Ranunculus lingua	—					I +
Verb.- u. Ordn.-Kennarten Brometalia:						
Galium verum	III		4 +–2	—		—
Trifolium montanum	II	—	2 +–1	—		—
Koeleria pyramidata	II		—		—	—
Bromus erectus	I		—	—	—	—
Euphorbia cyparissias	I	—	—	—	—	—
Trifolium ochroleucum	I	—	—	—		—
Hippocrepis comosa	I	—	—	—		—
Helianthemum ovatum	I	—	—	—		—
Filipendula hexapetala	—	—	1 +	—		—
Arten der Oxycocco-Sphagnetea:						
Myrica gale	—	—	—	II 1–2	1 +	IV +–
Drosera rotundifolia	—	—	—	—	2 +	II 1–2
Andromeda polifolia	—		—	I 1	—	—
Oxycoccus paluster	—	—	—	I 1	—	—
Scirpus caespitosus	—	—	—	I 1	—	—
Aulacomnium palustre	—	—	—	—	—	III +–
Feuchtigkeitszeiger (Diff.-Arten der Ges. welche hygrophiler sind als Molinion):						
Iris pseudacorus	—	3 +–2	—	—	1 +	—
Scutellaria galericulata	—	—	—	I 1	—	I +
Calamagrostis canescens	—	—	—	—	2 +–1	V +–
Lysimachia thyrsiflora	—	—	—	—	—	II +
Sphagnum palustre	—	—	—	—	3 3–5	I +
Sphagnum fimbriatum	—	—	—	—	1 +	II 2–3

	1	2	3	4	5	6
copus europaeus	—	—	—	—	1 +	—
tricularia minor	—	—	—	—	—	I 1
rex rostrata	—	—	—	—	—	I 2
hagnum squarrosum	—	—	—	—	—	I +
yopteris thelypteris	—	—	—	—	—	I 2
ockenheitszeiger:						
a pratensis	III	—	I +	—	—	—
ontodon hispidus	III	—	4 +–2	—	—	—
tus corniculatus	II	—	4 +–2	—	—	—
hillea millefolium	II	—	2 +	—	—	—
grostis tenuis	II	—	4 +–2	—	—	—
ypochoeris radicata	II	—	1 +	—	—	—
uscuta epithymum	I	—	2 +	—	—	—
hymus pulegioides	I	—	1 +	—	—	—
uzula campestris	—	—	4 +–1	—	—	—
nonis arvensis	—	—	3 +–2	—	—	—
nstige 2)						
crocladium cuspidatum	III	—	3 +	I +	3 +–3	IV 2–3
nthoxanthum odoratum	V	—	4 1–2	—	4 +–1	IV +–2
stuca rubra	III	—	3 1–2	—	4 +–1	III +
arex "lepidocarpa"	—	1 +	3 +	I +	—	—
lnus glutinosa	—	—	—	I 1	1 +	III +
alix aurita	—	—	1 +	—	1 +	I +
seudoscleropodium purum . .	—	—	1 +	—	3 1–3	I +
grostis stolonifera	III	—	2 +	—	—	—
etula pubescens	—	—	—	—	3 +	II +
alix cinerea	—	—	—	—	1 +	III +–1
juga reptans	I	—	1 +	—	—	—
agina procumbens	—	—	1 +	—	—	I +

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1) Von Zarzycki als Assoziations-Kennarten betrachtet.

2) Die nur in einem Gebiet erwähnten Arten, deren soziol. Zugehörigkeit Zweifelhaft ist, werden nten gesondert aufgeführt.

inmal sind erwähnt:

palte 1: Ranunculus nemorosus, Vicia tetrasperma ssp., Dactylis glomerata, Carex appropinquata, Mentha arvensis.

palte 2: Eleocharis uniglumis, Orchis palustris.

palte 3: Daucus carota, Salix rosmarinifolia, Thuidium delicatulum, T. abietinum, T. philiberti, Brachythecium sp., Campylium sp., Mnium cuspidatum, Carex contigua, Plantago media, Ctenidium molluscum, Hylocomium splendens, Cladonia furcata.

palte 4: Primula farinosa, Viola uliginosa, Juncus nodulosus, Campylium elodes, Cinclidium stygium, Sphagnum warnstorffii, S. contortum, Sesleria coerulea, Picea abies, Carex "oederi", Plagiochila asplenioides, Viola epipsila, Valeriana excelsa.

palte 5: Rubus sp., Lophocolea bidentata.

palte 6: Marchantia polymorpha, Mnium affine, Leptobryum pyriforme.

Es fällt auf, das *Carex hostiana* hier also dominiert in einer Gesellschaft der *Scheuchzerio-Caricetea,* wie in Mitteleuropa, doch im Gegensatz zu den niederländischen Verhältnissen. Ob das Verhalten in den Niederlanden als eine atlantische Erscheinung zu betrachten wäre, ist zweifelhaft, da ALLORGE und GAUME (zit. bei ISSLER 1934) *Carex hostiana* in Frankreich ebenfalls in Gesellschaften der *Scheuchzerio-Caricetea fuscae* erwähnen. In der schwedischen Gesellschaft ist der Hochmoorcharakter *(Oxycocco-Sphagnetea)* durch das Auftreten von *Andromeda polifolia* und *Oxycoccus paluster* noch stärker ausgeprägt als in den Niederlanden, wo diese Arten zwar vorkommen, aber niemals mit *Carex buxbaumii* vergesellschaftet sind.

Obwohl in der schwedischen Gesellschaft die "Klassenkennarten der *Molinieto-Arrhenatheretea*" sowie die *Agropyro-Rumicion*-Arten ganz fehlen und die *Phragmitetalia*-Arten nur schwach vertreten sind, gibt es hier doch einige mehr anspruchsvolle Arten wie *Vicia cracca, Scutellaria galericultata* und *Caltha palustris.*

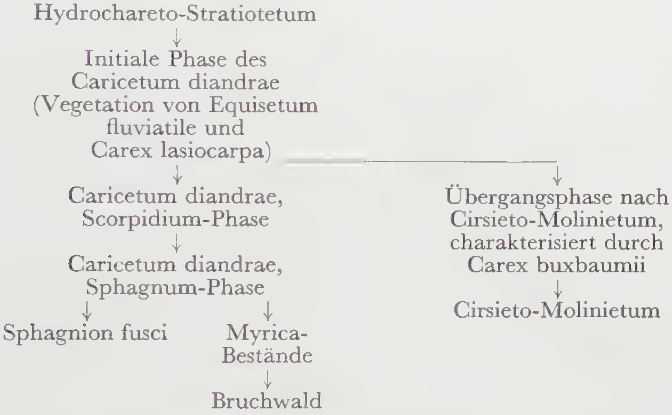
Es darf aus dieser einen Tabelle von ALMQUIST selbstverständlich nicht der Schluss gezogen werden, dasz *Carex buxbaumii* in Schweden nicht auch in anderer Vergesellschaftung auftreten könnte. Jedoch tritt aus diesem regionalen Vergleich als Tendenz hervor, dasz *Carex buxbaumii* vom Süden nach Norden und vom Osten nach Westen in allmählich nährstoffärmeren und zugleich allmählig nässeren, im Sommer weniger stark austrocknenden Standorten gedeiht.

2. NÄHERE BETRACHTUNG DES NIEDERLÄNDISCHEN MATERIALS (Tabelle II)

Von den niederländischen Lokalitäten der *Carex buxbaumii* ist diejenige bei Wanneperveen in N.W.-Overijsel, wie schon erwähnt, die meist ausgedehnte und differenzierte; die vegetationskundliche Stelle der Art lässt sich hier am Besten beurteilen. Wir werden also die Aufnahmen 7–20 der Tabelle II, welche sich auf diesem Fundort beziehen, zuerst besprechen.

Die erwähnte Gegend ist ein Sumpfgebiet von mehreren hundert Hektar, in welchem *Carex buxbaumii* auf etwa 200 ha an mehreren Stellen auftritt. Die Aufnahmen 7–13 geben diese verschiedene Kleinfundorte gesondert wieder; die Aufnahmen 14–20 entstammen einem Transsect von Aufnahmen an eine dieser Stellen, die sog. "Maatjes". Die Struktur der Landschaft ist folgende. Die Parzellierung ist lang und schmal; zwischen mehr oder weniger parallel verlaufenden Streifen alten, nicht oder nicht rezent abgestochenen Torfbodens, mit Streuwiesen bewachsen ("ribben" oder "legakkers") finden sich Torfstiche, welche in Tiefe und Umfang sehr verschieden sind. Die kleinsten Torfstiche sind nur einige m² gross; die grösseren jedoch bilden ausgedehnte Sumpfe und sind hier und da im Laufe der Geschichte eben zu seichten, Kwadratkilometergrossen Seen ausgewachsen. In diesen Torfstichen haben sich Verlandungsserien ausgebildet, welche zu Schwingrasen führen; diese können sich entweder zum Erlen- oder Birkenbruchwald entwickeln, oder, wenn sie jährlich gemäht werden, zu einer Hochmoorgesellschaft mit *Erica tetralix,* *Oxycoccus paluster, Polytrichum strictum, Aulacomnium palustre* usw. In seltenen, unten näher zu besprechen Fällen kann die Sukzession vom Schwingrasen zum *Cirsieto-Molinietum* führen.

Die Vegetationsverhältnisse dieses Gebietes (und der ähnlichen umringenden Gegenden) sind zuerst von Van Dijk & Westhoff (1955) beschrieben worden, nachher von Kuiper & Segal (1955) und Kuiper (1958) genau analysiert worden. Kuiper (1958) hat gezeigt, dasz der Charakter der Verlandungsserie von Ausmass und Tiefe der Ausgangsstandorten abhängt. Wir werden uns hier beschränken auf dem meist typischen Fall:


Hydrochareto-Stratiotetum
Initiale Phase des Caricetum diandrae (Vegetation von Equisetum fluviatile und Carex lasiocarpa)
Caricetum diandrae, Scorpidium-Phase
Caricetum diandrae, Sphagnum-Phase
Sphagnion fusci
Myrica-Bestände
Bruchwald
Übergangsphase nach Cirsieto-Molinietum, charakterisiert durch Carex buxbaumii
Cirsieto-Molinietum

Das optimale *Caricetum diandrae* ist eine sehr artenreiche, homogene Schwingrasengesellschaft mit einer grossen Zahl charakteristischen Arten, wie *Carex diandra, Eriophorum gracile, Calamagrostis neglecta, Utricularia intermedia, Parnassia palustris, Liparis loeselii, Sagina nodosa, Campylium stellatum, Scorpidium scorpioides, Drepanocladus intermedius, Brigum pseudotriquetrum, Philonotis fontana, Fissidens adiantoides, Riccardia multifida, R. sinuata, R. pinguis*, vergesellschaftet von konstanten Arten wie *Pedicularis palustris, Menyanthes trifoliata, Comarum palustre, Carex lasiocarpa, Valeriana dioica, Viola palustris, Dactylorchis majalis, D. praetermissa*. Ein Teil dieser Arten tritt auch im *Cirsieto-Molinietum* auf, doch charakteristische *Molinietalia*-Arten sind in diesem Stadium noch kaum da. In dieser Assoziation fehlt *Carex buxbaumii;* sie ist daher in Tabelle II nicht vertreten.

Der Schwingrasen steigt und sinkt mit dem Wasserniveau und ist daher konstant nass. Es gibt aber Stellen, wo die ursprünglich schwimmende Vegetation an den unabgestochenen alten "legakkers" (Moorbodenstreifen) anwächst. Den "legakkers" entlang kann es somit ein Sumpfstreifen geben, dessen Oberfläche den Grundwasserwechsel nicht mehr folgt. Es ist zu erwarten, dasz in diesem Fall Wechselfeuchtigkeitszeiger eintreten werden, also Arten des *Cirsieto-Molinietum.* Dies ist tatsächlich der Fall: es erscheinen *Carex pulicaris, C. hostiana, Sanguisorba officinalis, Carex panicea, Viola stagnina, Dactylorchis incarnata,* und auch *Carex buxbaumii. Carex buxbaumii* zeigt von diesen Arten die

TA

Carex buxbaumii in den Niederl

Erläuterung:

E = Elzas (Ried d'Herbsheim)
M = Meppel (Kierse Wiede)

R = W. J. Reijnders
D = J. van Dijk

Innerhalb der Einzelgebieten sind die Aufnahmen geordnet nach abnehmender Artenzal
Caricetalia fuscae.

Nr.	1	2	3	4	5
Gebiet	E	Nieuwkoop			
Verfasser	W	R	R	W	W
Jahr (19..)	55	49	49	57	57
Datum	23 V	20 VI	4 VI	4 VI	4 VI
Probefläche in m²	20	10	9	150	10
Krautschicht, Bedeckung in %	100	70	60	100	80
Moosschicht, Bedeckung in %	10	100	100	100	100
Carex buxbaumii	3.2	3.2	2.2	3.5	2.2
Kennarten des Cirsieto-Molinietum:					
Carex pulicaris	—	—	—	—	—
Cirsium dissectum	—		—	—	—
Viola stagnina	2.2		—	—	—
Cirsium spurium	—	—	—	—	—
Viola ritschliana	+.2	—	—	—	—
Carex hostiana		—	—	—	—
Verbands-Kennarten Molinion:					
Thalictrum flavum	+.1	+.1	—	+.1	+.1°
Succisa pratensis	—	2.3	—	2.1	—
Gentiana pneumonanthe	1.1	—	—	—	—
Ordnungs-Kennarten Molinietalia:					
Lythrum salicaria	+.1	+.1	—	+.1	1.1
Sanguisorba officinalis	+.1	—	—	—	—
Cirsium palustre	—	+.1	1.1	+.1	+.1
Luzula multiflora	—	+.2	1.2	+.2	+.2
Rhinanthus glaber	—	+.1	—	+.2	+.1
Juncus conglomeratus	—	—	—	+.1	—
Lychnis flos-cuculi	—	—	1.1	+.1	+.1
Lotus uliginosus	—	+.1	1.1	+.1	+.1
Achillea ptarmica	—	—	—	—	1.2
Juncus acutiflorus	—	—	—	—	—
Verbands- und Ordn.-Kennarten Scheuchzerio-Caricetea fuscae:					
Comarum palustre	—	2.2	—	+.2	—
Carex diandra	—	—	—	—	—
Viola palustris	—	—	—	+.2	—
Menyanthes trifoliata	—	—	—	—	—
Pedicularis palustris	—	+.1	—	1.2	1.1
Juncus subnodulosus	—	+.1	—	2.2	1.2
Carex lasiocarpa	—	—	—	—	—
Bryum ventricosum	—	—	—	—	—
Carex curta	—	—	—	—	—
Carex nigra	—	—	—	—	—
Stellaria palustris	—	—	—	—	—

t einer Aufnahme aus dem Elsass)

S. Segal DW = J. van Dijk und V. Westhoff
V. Westhoff

ei einigen Moosen) bedeutet, dasz die Art in der Aufnahme vorkommt, dasz jedoch die danz–Dominanz nicht bekannt ist.

8	9	10	11	12	13	14	15	16	17	18	19	20
Vanneperveen, verschiedene Lokalitäten						Wanneperveen, Transsect "Maatjes"						
DW	S	DW	DW	D	S	S	S	S	S	S	S	S
58	54	55	55	54	58	58	58	58	58	58	58	58
15		3	7		29	20	20	20	20	20	20	20
VIII	VI	VIII	VI	VI	VI	VII	VII	VII	VII	VII	VII	VII
8	10	100	15	5	4	15	5	3	3	6	2	10
100	95	100	100	90	95	60	90	60	100	95	100	95
100	50	70	30	40	50	×	×	×	×	×	×	×
2.1–2	+.2	2.1	2.2	2.2	+.2	+.1	1.2	1–2.2	+.1	1.1	1–2.2	+.2
1.2	2.3	—	—	+–1.2	—	+.2	+.2	—	—	+.2	—	—
—	—	—	1.1	1.1	+.1	—	2.1	—	—	—	+.1	+.2
—	—		1.2	1.1–2	—	—	—	—	—	—		—
—	—		+.1	—	+.1	—	+.1	—	—	—	—	—
—	—		—	+.1	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	+.1	—			—	—
—	—	—	+.1	+.1	+.1	+.1	+.1	+.1	—	+–1.1	+.1	—
—	+.1	1.1	1.2	+–1.2	+.1	—	+.1	—	—	+.1	—	1.2
—	—	—	—	—	—	—	—	—	—	—	—	—
1.1	+.1	+.1	+.1	+.2	1.1	—	+.1	—	+.1	+.1	+.1	+.1
1.1	1.1	+.1	1.2	2–3.2	+.1	+.1	+.1	+.1	+.1	+.1	+.1	2.1
1.1	+.1	—	+.1	+.1	+.1	—	+.1	—	1.1	+.1	+.1	+.1
+.1	+.2	—	+.2	+–1.1	+.2	—	+.1	+.1	—	+.1	+.1	+.1
1.1	—	—	—	—	—	2.2	+.1	+.1	—	2–3.2	—	—
+.2	—	—	+.1	+.1	2.2	—	—	—	+.2	—	+.2	+.2
+.1	—	—	1.2	—	+.1	—	—	—	—	—	—	—
2.1–2	—	+.2	+.1	—	+.2	—	—	—	—	—	—	—
+.1	—	+.1	+.1	+.1	—	—	—	—	—	+.1	—	—
—	—	—	+.2	—	—	—	—	—	—	—	—	—
1.1	+.1	2.2	+.1	+.1	+.2	2.1	—	1.2	+.2	+.1	—	—
1.1	2.2	3.5	—	+.1	—	3.2	+.2	+.2	1.2	1.2	+.2	+.2
+.2	+.1	1.1	1.2	—	—	—	+.1	—	1.1	1.1	+.1	—
2.2	2.1	3.3	—	2.2	—	3.4	—	3.2	2.2	2.2	3.1	—
+.1	1.2	—	—	—	—	+–1.2	—	+.2	—	—	+.1	—
2.2	—	—	—	—	1.2	—	—	—	2–3.2	—	—	+.2
1.1	—	2.5	—	—	+.2	+.1	+.2	—	—	+.2	—	—
1.2	—	—	+.2	—	—	+.1	—	—	—	—	—	—
+.2	—	—	+.2	—	+.2	—	—	—	—	—	—	—
—	+.1	—	—	—	—	—	+.2	—	—	—	—	+.2
+.1	+.1	—	+.1	—	—	—	—	—	—	—	—	—

Nr.	1	2	3	4	5
Epilobium palustre	—	+.1	—	—	—
Sagina nodosa	—	+.1	—	+.1	—
Liparis loeselii	—	—	—	+.1	—
Eriophorum gracile	—	—	—	—	—
Campylium stellatum	—	—	—		—
Scorpidium scorpioides	—	—	—	—	—
Drepanocladus intermedius	—	—	—	—	—
Riccardia pinguis	—	—	—	—	—
Riccardia multifida		—	—	—	—
Gemeinschaftliche Arten Molinietalia und Scheuchzerio-Caricetea fuscae:					
Valeriana dioica	—	1.1	1.1	2.2	2.2
Hydrocotyle vulgaris	+.2	1.2	—	+.2	—
Mentha aquatica	—	+.1	+.1	—	+.1
Agrostis canina	—	—	—	—	1.2
Galium uliginosum	—	+.2	2.1	1.2	2.2
Dactylorchis incarnata	—	—	—	—	—
Calamagrostis neglecta	—	—	—	—	—
Dicranum bonjeani	—	—	—	2.2–3	2.3
Carex demissa	—	—	—	1.2	+.2
Juncus articulatus	—	—	—	+.2	—
Hierochloë odorata	—	+.1	+.1	+.2	—
Parnassia palustris	—	—	—	—	—
Ranunculus flammula	—	—	—	—	—
Gemeinsch. Arten Molinietalia, Scheuchzerio-Caricetea fuscae u. Brometalia:					
Fissidens adiantoides	—	—	—	—	—
Linum catharticum	—	—	—	—	—
Leontodon nudicaulis	—	1.2	—	—	—
Briza media	—	—	—	—	—
Differentialarten Molinietalia geg. Arrhenatheretalia:					
Molinia coerulea	4.3	+.1	2.1	2.3	2.3
Peucedanum palustre	—	+.1	+.1	+.1	+.1
Galium palustre	+.2	—	+.1	—	+.2
Carex panicea	2.2	—	—	+.2	+.2
Lysimachia vulgaris	—	+.1	—	+.1	+.1
Pellia epiphylla	—	—	—	—	—
Sphagnum recurvum	—	—	—	—	—
Juncus effusus	—	—	1.1	—	—
Chiloscyphus polyanthus	—	—	—	—	+.2
Symphytum officinale	1.1	—	—	—	—
Verbandskennarten Calthion u. Filip.-Petasition:					
Lathyrus paluster	—	—	2.1	+.1	—
Filipendula ulmaria	—	+.1	—	+.1	1.2
Angelica sylvestris		+.1	+.1	+.1	+.1
Valeriana officinalis	—	+.1	2.1	+.1	—
Dactylorchis praetermissa ssp. junialis	—	—	—	+.1	+.1
Dactylorchis praetermissa	—	+.1	—	+.1	+.1
Carex disticha	—	—	—	—	—
Hypericum tetrapterum	—	+.1	—	+.1	—
Caltha palustris	—	—	—	—	—
Dactylorchis majalis	—	—	—	—	—
Senecio aquaticus	—	—	—	—	—

8	9	10	11	12	13	14	15	16	17	18	19	20
+.1	—	—	—	—	—	—	—	—	—	—		-
—	—	-	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—		—	—
—	—	—	—	—		—	—	—		—	—	—
—	—	—	—	—	—	—	—	—	—		—	—
—	—	—	—	—	—	—	—	—		—	—	—
-	—	—	—	—	—	—	—	—	—	—	—	—
-	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—		—	—		—	—	—
2.2	2.1	2.2	+.1	1.2	+.1	—	+.1	+.2	+.1	2.2	1.1	—
2.2	—	2.2	1.1	—	1.2	+.2	+.1	+.2	1.2	1.2	+.1	+.2
1.1	+.1	1.1	1.1	—	+.2	+.2	1.1	+.2	—	1–2.2	+.2	+.1
2.2	—	1.2	2.4	1.2	2.2	+.2	2–3.3	1.2	3–4.4	2.3	1–2.2	2.3
1.1–2	—	+.2	1.2	+.1	+.2	—	+.2	—	—	—	—	—
—	+.1	+.1	—	+.1	(+)	1.1	+.1	+.1	—	+.1	+.1	—
1–2.2	1.1	1.1	+.2	+–1.1	(+)	—	—	+.1	—	—	—	—
—	—	—	—	2.3	—	—		—	×	—	×	×
—	—	—	—	+.2	-	—	+.3	—	—	—	—	+.2
—	—	—	—	—	+.2	+–1.2	—	+.1	—	—	—	—
—	—	—	1.1	—	+.1	—	—	—	—	—	—	—
—	+.1	1.1	—	—	—	—	—	—	—	+.1	—	—
—	—	—	—		-	+.1	—	—	—	—	—	+.1
+.2	—	—	+.2	—	+.1	+.1	—		×	—	—	×
—	—	+.1	—	—	—	+.2	—	+.2	—	—	—	—
—	—	—	—	—	+.2	—	—	-	—	—	—	—
+.2	-	—	—	—	—	—	—	—	—	—	—	—
3.2	—	1.2	3.3	4.4	+.2	1.2	4.5	1.2	2.2	4–5.5	+–1.2	5.5
+.1	+.1	1.1	+.1	+.1	+.1	+.2	-	-	+.1	+.1	+.1	+.1
+.1	+.1	+.2	+.1	+.1	—	+.1	+.1	—	+.2	—	+.1	+.2
1.2	1.3	+.2	2.2	+.1	3–4.4	2.2	1–2.2	3.2	-	1.2	—	—
—	—	—	1.1	+.1	+.1	—	+.1	—	+.1	+.1	+.1	—
1.2	—	1.2	—	—	—	—	—	—	—	—	—	—
4.4	—	4.5	—	—	-	—	—	—	—	—	—	—
—	—	—	—	—	+–1.2	—	—	—	—	—	—	—
—	—	—	+.2	—	—	—	—	—	—	—	—	—
—	—	—	+.1	—	—	—	—	—	—	—	—	—
+.2	+.1	—	+.1	—	+.1	—	+.1	—	+.1	+.1	—	—
+.2	+.1	+.1	1.2	+.2	+.1	—	—	—	—	+.1	—	-
+.1	—	—	+.1	—	+.1	—	—	—	+.1	—	+.1	+.1
+.2	—	+.1	+.2	+.1	+.1	—	+.1	—	—	—	—	—
+.1	+.1	—	—	—	—	+.1	—	—	—	+.1	—	—
+.1	—	+.1	—	—	—	+.1	—	—	—	—	—	—
1.1	—	—	—	+.2	—	—	+.2	—	+.2	—	—	—
+.1	—	—	+.1	—	+.1	—	—	—	—	-	-	-
+.1	—	—	—	—	—	—	—	—	-	—	—	—
—	+.1	-	—	—	—	—	—	—		—	—	—
—	—	—	—	-	—	—	—	—	—	—	—	—

Nr.	1	2	3	4	5
Gemeinsch. Arten Filip.-Petasition u. Senecion fluviatilis:					
Eupatorium cannabinum	—	+.1	+.1	+.1	+.1
Calystegia sepium	—	—	+.1	+.1	+.1
Senecio paludosus	1.1	—	—	—	—
Verb.- u. Ordn.-Kennarten Arrhenatheretalia:					
Vicia cracca	—	—		+.1	+.1
Trifolium repens	—	—		—	—
Cynosurus cristatus	—	—	—	—	—
Galium mollugo	—	—	—	—	—
Lathyrus pratensis	+.2	—		—	—
Gemeinsch. Arten Molinietalia u. Arrhenatheretalia (sog. Klassenkennarten d. Molin.-Arrhenatheretea)					
Holcus lanatus	—	—	1.2	+.2	1.1–2
Rhytidiadelphus squarrosus	—	—	5.5	+.2	2.2
Prunella vulgaris	—	+.1	—	+.1	+.1
Plantago lanceolata	—		—	—	—
Cardamine pratensis	—	—	—	—	—
Rumex acetosa	+.1	—	+.1	—	+.1
Ranunculus acer	—	—	—	—	—
Climacium dendroides	1.2	—	—	—	—
Verbands- u. Ordn.-Kennarten Nardetalia:					
Potentilla erecta	+.2	2.2	+.2	1.2	2.2
Sieglingia decumbens	—	—	—	—	
Potentilla anglica				—	—
Viola canina			—	—	—
Polygala vulgaris	—	—	—	—	—
Platanthera bifolia	—	—	—	—	
Verbands-Kennart Agropyro-Rumicion crispi:					
Ranunculus repens	1.2	—	—	—	—
Verb.-K.A. Magnocaricion u. Ordn.-K.A. Phragmitetalia:					
Phragmites communis	—	2.2°	1.1°	2.1°	2.1°
Equisetum fluviatile	—	—	1.1	+.1	—
Carex acutiformis	—	+.2	—	—	—
Carex acuta	—	—	—	—	—
Carex hudsonii	—	—	—	—	—
Poa palustris	—	—	—	—	—
Typha angustifolia	—	—	+.1	—	—
Ranunculus lingua	—	—	—	—	—
Arten der Oxycocco-Sphagnetea:					
Myrica gale	—	+.1	—	—	—
Aulacomnium palustre	—	—	—	—	—
Drosera rotundifolia	—	—	—	+.2	+.2
Feuchtigkeitszeiger (Diff.-Arten der Ges. welche hygrophiler sind als Molinion):					
Calamagrostis canescens	—	—	1.2	(+.1)	—
Dryopteris thelypteris	—	—	—	+.1	+.2
Sphagnum palustre	—	5.5	—	3.3	3.4
Sphagnum fimbriatium	—	—	—	+.3	—
Lysimachia thyrsiflora	—	—	—	—	—
Lycopus europaeus	—	—	+.1	—	—
Iris pseudacorus	1.2	+.1	—	—	—

8	9	10	11	12	13	14	15	16	17	18	19	20
+.1	—	+.1	+.1	—	—	—	—	—	—	—	—	+.1
—	—	—	—	—	—	—	—	—		—	—	—
—	—	—	—	—	—	—	—	—		—	—	—
	—	—	—	—	—	—	—	—		—	—	—
—	—	—	—	—	—	—	—	—		—	—	—
—	—	—	—	—	—	—	—	—		—	—	—
—	—	—	—	—	+.1	—	—	—	—	—	—	—
—	—	—	—		—	—	—	—	—	—	—	—
+.2	+.2	1.1	+.2	+–1.2	2.2	—	+.2	—	+.2	1.1	+.2	2.2
+.2	2–3.3	—	—	2–3.3	—	+.2	×	—		×	×	×
+.1	—	+.1	—	+.1	—	—	+.1	—	—	+.1	—	+.1
+.2	—	—	+.2	+.1	+.2	—	+.1	—	—	—	—	+.1
+.1	—	—	+.1	—	+.1	—	—	—	—	—	—	—
—	—	—	—	—	+.1	—	—	—	—	—	—	—
+.1	—	—	+.1	—	—	—	—	—	—	—	—	—
+.2	—	—	—	—	—	—	—	—		—	—	—
+.2	—	+.2	1.2	—	+.1	+.2	+.2	+.2	+.2	—	+.2	1.1
—	—	—	—	+–1.2	+.1	—	+.2	—	+.1	—	+.1	+.1
—	+.1	—	—	+.2	—	—	+.2	—		—	—	—
—	—	—	—	+–1.1	+–1.2	—	1–2.2	—		+.2	+–1.2	1.2
—	—	—	—	+.1	—	—	—	—	—	—	—	—
—	—	—	—		+.1	—	—	—		—	—	—
—	—	—	—		—	—	—	—	—	—	—	—
+.1°	+.1°	1.1°	1.1°	+.2°	2–3.2	+.1°	+.2°	+.1	1.1–2	+.1°	+.1°	2.2°
+.1	1.1	2.1	+.1	+–1.1	+.1	+.1	+.1	+.1	+.1	1.1	+.1	+.1
—	—	—	—	—	—	+.2	+.2	+.2	2–3.2	+–1.2	3.4	—
1.2	—	—	—	+.1	(+)	—	—	—	—	—	—	—
+.2	—	+.2	—		—	—	—	—		—	—	—
—	—	—	—	—	+.1	—	—	—	—	+.2	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	+.1	—	—	—	—	—	—		—	—	—
2.2	1.1	1.2	+.1	—	+.2	+.2	—	+.2		+.2	—	—
2.2	—	1.2	1.2	—	—	—	×	—		—	—	×
1.1	—	2.1–2	—	—	—	—	—	—	—	—	—	—
+.2	1.1	+.2	1.2	—	—	—	—	—	2–3.2	—	—	+.2
—	—	—	2.1	—	1.2	—	—	—	—	+.2	—	—
+.3	—	+.3	—	—	—	—	—	—		—	—	—
3.3	—	2.3	—	—	—	×	—	—	—	—	—	—
+.1	+.1	—	—	+.1	—	—	+.1	—	—	—	—	—
—	—	—	+.1	—	+.1	—	—	—		—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—

Nr.	1	2	3	4	5
Utricularia minor	—	—	—	—	—
Sphagnum squarrosum	—	—	—	—	—
Scutellaria galericulata	—	—	—	—	—
Carex rostrata	—	—	—	—	—
Sonstige (insofern mehr als einmal):					
Anthoxanthum odoratum	—	1.2	+.2	+.2	1.1
Acrocladium cuspidatum	—	—	+.2	3.3	1.2
Festuca rubra	—	+.2	1.2	+.2	+.2
Scleropodium purum	—	—	1.2	2.3	3.3
Alnus glutinosa	—	—	—	+.1	—
Betula pubescens	—	—	+.1	+.2	+.1
Salix cinerea	—	—	—	—	1.2
Salix aurita	—	—	—	—	+.1
Frangula alnus	—	—	—	—	—

Ausserdem wurden einmal beobachtet:

in Nr. 1: Oenanthe peucedanifolia (1.2), Filipendula hexapetala, Mentha arvensis, Stach palustris.
in Nr. 3: Mnium hornum (1.2).
in Nr. 5: Lophocolea bidentata.
in Nr. 6: Sagina procumbens, Mnium affine (1.2).
in Nr. 11: Campylium polygamum, Taraxacum sp.
in Nr. 12: Rubus sp.
in Nr. 13: Agrostis stolonifera (1–2.2), Calypogeia trichomanis (3.3), Brachythecium rutabulu (2.2), Ceratodon purpureus.
in Nr. 17: Atrichum undulatum.

engste Amplitude: sie ist ausschliesslich an diesem Stadium gebunden. Auch die ökologisch viel weiter verbreitete *Carex disticha* zeigt eine Preferenz für diesen Übergangsstreifen, wie es auch in Schweden beobachtet wurde (Du Rietz c.s. 1939). Kuiper (1958) meint eben, dasz *Carex buxbaumii* verschwindet, sobald die Arten der "mehr saueren Endstadien" *(Oxycocco-Sphagnetea*-Arten) einsetzen; unsere Tabelle zeigt aber, dasz sie sich auch in diesem Fall noch gut halten kann. Abgesehen von dieser Tendenz zum Hochmoor tritt in dieser Sukzession später auch *Molinia coerulea* auf; sobald diese zu dominieren anfängt, kann auch *Cirsium dissectum* erscheinen und verringert die Artenzahl der *Scheuchzerio-Caricetea fuscae* sich stark. Dieses Stadium stellt das typische "*Cirsieto-Molinietum caricetosum buxbaumii*" dar.

Die Aufnahmen 7–20 der Tabelle II zeigen, dasz die höhere oder geringere Abundanz der *Carex buxbaumii* nicht mit Ansteigen oder herabsinken der Dominanz von *Molinia coerulea* korreliert ist. Es besteht zwischen den beiden Arten weder eine positive noch eine negative (Konkurrenz-) Affinität. Nichtsdestoweniger fehlt *Carex buxbaumii* vollstandig in alten Beständen des *Cirsieto-Molinietum typicum*, in den die Artengruppe der *Scheuchzerieto-Caricetea fuscae* stark zurückgetreten ist. Wenn Kuiper (1958) vermutet, dasz diese Erscheinung mit der starken Versäuerung im alten und typischen *Cirsieto-Molinietum* zusammenhängt, hat er wohl recht. *Carex buxbaumii* kann also nicht in den Schwingrasen wächsen, weil sie Wechselfeuchtigkeit bedürft, aber

8	9	10	11	12	13	14	15	16	17	18	18	20
—	+.2	—	—	—	—	—	—	—	—	—	—	—
+.2	—	—	—	—	—	—	—	—	—	×	—	—
—	—	—	+.2	—	—	—	—	—	—	—	—	—
—	—	—	—	—		—	—	—	—	—	—	—
+.2	—	—	2.2	1.2	1.2	+.1	+.2	+.1	+.1	—	+.1	+.1
2.2	3.4	—	2.3	3.4	+.2	+.2	×	×	×	—	—	—
+.2	—	—	—	+-1.2	—	—	+.2	—	+.2	+.2	+.2	+.2
+.1	—	—	—	—	—	—	×	—	—	×	×	×
—	+.1	+.1	—	—	—	—	—	—	—	+.1	—	—
+.1	—	—	—	—	—	—	—	—	—	—	—	—
+.1	—	—	+.1	—		—	—	—	—	—	—	—
—	—	—	+.1	—	—	—	—	+.1	—	+.1		—
—	—	—	+.1	—	+.1	—	—	—	—	—	—	—

auch nicht in den älteren wechselfeuchten *Molinieten*, insoweit diese nicht mehr von etwas nährstoffreicherem Wasser überflutet werden. Sie ist auf ein ganz bestimmtes Stadium beschränkt.

Vergleichen wir nun mit diesen Ergebnissen die Verhältnisse der anderen Lokalitäten von *Carex buxbaumii* in den Niederlanden.

In der ziemlich artenarmen Aufnahme 6 (Kierse Wiede, Meppel), in der *Carex buxbaumii* allerdings reichlich vertreten und optimal entwickelt war, fehlen sowohl die Assoziationskennarten des *Cirsieto-Molinietum* und Verbandskennarten des *Molinions* wie die Differentialarten der *Molinietalia*, fast alle Kennarten der *Scheuchzerio-Caricetea fuscae* und alle Arten der *Nardetalia* und der *Oxycocco-Sphagnetea*. Dagegen sind die *Molinieto-Arrhenatheretea*-Arten gut vertreten, *Plantago lanceolata* eben mit 3.1, und finden sich hier *Lolieto-Cynosuretum*-Arten: *Trifolium repens* und *Cynosurus cristatus*, und eine *Agropyro-Rumicion*-Art: *Ranunculus repens*. Auch *Carex acuta* mit 3.5 deutet auf Nährstoffreichtum. Es händelt sich hier um einen Bestand, der vor einigen Jahren einmal mit Kunstdünger bearbeitet wurde. Nachher ist das Gebiet aber von dem Naturschutz erworben und die Düngung verboten worden. In dieser relativ nährstoffreichen Umwelt kann *Carex buxbaumii* sich anscheinend sehr gut halten; wahrscheinlich ebenso in der Regression zum ursprünglichen "in Wechselfeuchtwerdung begriffenen Schwingrasen", die inzwischen eingesetzt hat.

Die Bestände aus Nieuwkoop (Tabelle II, Aufnahmen 2-5) sind denjenigen aus Wanneperveen mehr ähnlich, aber deutlich artenärmer. Diese Armut ist in erster Linie pflanzengeographisch bedingt: Arten wie *Calamagrostis neglecta*, *Sanguisorba officinalis*, *Parnassia palustris* fehlen in den südholländischen Sumpfgebieten völlig. Das fehlen der Assoziationskennarten des *Cirsieto-Molinietum* kann aber nicht in dieser Weise erklärt worden: sie finden sich in kurzer Nähe. Die Bestände der *Carex buxbaumii* sind wohl auch etwas kulturbeeinflusst: Aufnahme 2 kaum, Aufnahme 3 (*Rhytidiadelphus squarrosus* 5.5!) aber deutlicher. Letztere zeigt auch Anklänge an der Hochstaudenflur des *Valerianeto-Filipenduletum* (*Lathyrus paluster* 2.1, *Valeriana officinalis* 2.2).

Carex buxbaumii gedeiht in dieser Vergesellschaftung optimal. Sie erreicht in zwei Aufnahmen eben die Dominanz 3; in N.W.-Overijsel ist mit 2 das Maximum schon erreicht.

SUMMARY

On the ecology of Carex buxbaumii Wahlenb. in Europe, especially in the Netherlands

Carex buxbaumii is a circumboreal species, rather rare in Fennoscandia and C.-Europe, very rare and scattered in Western Europe. It is characteristic of sedge swamps in succession to litter fen with oscillating phreatic level. Its ecological amplitude however seems not to be quite similar all over Europe. For an analysis of such differences vegetation tables (method of Braun-Blanquet) from E.-France, S.-Germany, Poland, the Netherlands and Sweden are summarised and compared in table I. Going from S to N and from E to W the species shows a tendency of preferring a more oligotrophic and moister habitat with a less oscillating water table. The dynamic and ecological position of the species within the Netherlands has been studied more in detail (table II).

LITERATUR

Almquist, E. 1929. Upplands vegetation och flora. Acta phytogeogr. suec. **1**: 624 S. + 431 Karten. Uppsala.

Cajander, A. 1935. Über die fennoskandischen Formen der Kollektivart Carex polygama Schkuhr. Ann. bot. soc. zool.-bot. fenn. Vanamo **5**: 5: 1–117.

Du Rietz, G. c.s. 1939. Zur Kenntnis der Vegetation des Sees Tåkern. Acta phytogeogr. suec. **12**: 65 S. + 7 Taf. Uppsala.

Dijk, J. van & V. Westhoff. 1955. De plantengroei der natuurgebieden in Noordwest-Overijsel. Natuur en Landschap. **9**: 33–57. Amsterdam.

Engel, R. 1953. Au sujet de Carex buxbaumii Wahlenb. Le monde des plantes **48**: 15–16. Toulouse.

Flora Batava 1901 **21**: 1625.

Goethart, J. W. C. 1905. De verarming der wilde flora en voorstellen om deze tegen te gaan. Ned. Kruidk. Arch. **15**: 49–69.

Hegi, G. o. J. Illustrierte Flora von Mitteleuropa **2**.

Hultén, E. 1950. Atlas of the distribution of vascular plants in NW-Europe. 512 S. Stockholm.

———. 1958. The amphi-atlantic plants and their phytogeographical connections. 340 S. Stockholm.

Issler, E. 1932. Les prairies non fumées du Ried ello-rhenan et le Mesobrometum du Haut-Rhin. 89 S. Colmar.

Kern, J. & Th. Reichgelt. 1954. Flora neerlandica **1**, 3. Carex L. 133 S. Amsterdam.

Koch, W. 1943. Carex Hartmani A. Cajander, eine für die Schweizerflora neue boreale Seggenart. Ber. schweiz. bot. Ges. **53**: 457–460. Bern.

Kuiper, P. 1958. Verlandingsvegetaties in N.W.-Overijsel. Kruipnieuws. **20**, 1: 1–20 + 5 Tabellen u. farb. Veg.-Karte. Wageningen.

——— & S. Segal. 1955. De natuurgebieden rondom de Belter- en Beulakerwijde. Kruipnieuws **17**, 3: 9–18. Amsterdam.

Lebrun, J., A. Noirfalise, P. Heinemann & C. Vandenberghen. 1949. Les associations végétales de Belgique. Bull. soc. roy. bot. belg. **82**: 105–207.

Oberdorfer, E. 1949. Pflanzensoziologische Exkursionsflora. 411 S. Stuttgart.

———. Süddeutsche Pflanzengesellschaften. Pflanzensoziologie **10**. 564 S. Jena.

Reijnders, W. J. 1949. Nieuwkoopse paradepaardjes. Kruipnieuws **11**, 4: 2–5. Wageningen.

Soest, J. L. van. 1933. De flora van de IJseldelta. Ned. Kruidk. Arch. **43**: 421–482.

Vandenberghen, C. 1951. Les prairies à Molinia en Belgique. Bull. soc. roy. bot. belg. **83**: 373–403.

Vlieger, J. 1937. Aperçu des groupements végétaux des Pays-Bas. Ned. Kruidk. Arch. **47**: 335–353.

Vuyck, L. 1899. Verslag van de 66e verg. v. d. Ned. Bot. Ver. Ned. Kruidk. Arch. 3e Ser. **1**, 4: 566–601.

Westhoff, V. 1947. The vegetation of dunes and salt marshes on the Dutch islands of Terschelling, Vlieland and Texel. 131 S. Den Haag.

———, J. W. Dijk, H. Paschier & G. Sissingh. 1946. Overzicht der plantengemeenschappen in Nederland. 118 S. Amsterdam.

Zarzycki, K. 1958. Wazniejsze zespoly lakowe doliny górnej Wisly a poziomy wod gruntowych (Die wichtigsten Gründlandgesellschaften des oberen Weichseltales und die Grundwasser-Ganglinien). Acta soc. botan. Poloniae. **27**: 3: 383–428.

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SOME REMARKS ON THE SMALL-FLOWERED FORGETMENOTS

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In early botanical history the conception of species concerning the small-flowered fortgemenots was still indefinite and uncertain. Even the genus *Myosotis* was only differentiated in 1719 by J. J. Dillenius from *Cerastium*, *Echium*, and *Alsine*. The latter genera were considered synonyms by authors such as M. Lobelius (1581) and C. Bauhin (1671). Similarly, C. Linnaeus did not differentiate between the small-flowered species of *Myosotis*. He records in his "Species Plantarum" (1753), besides species that are less relevant in this connection:

M. scorpioides: M. feminibus nudis foliorum apicibus callosis
  α arvensis
    Myosotis foliis hirsutis
  β palustris
    Myosotis foliis glabris.

Fortunately I had the opportunity to view some specimens of his collection. The Herbarium of the Hortus Cliffortianus (BM) contained *M. scorpioides α arvensis* and *M. scorpioides β palustris*. The former was a young plant, in early flower, but as far as foliage, hairiness and habit were concerned, it undoubtedly belongs to *M. arvensis* (L.) Hill. The Linnean Herbarium (LINN) contained some forgetmenots which are recorded in Savage's Catalogue as:

180, *M. scorpioides*
180, 2 K(alm)
180, 3 *M. foliorum apicibus callosis* Gmelin

After studying these plants I am of the opinion that they can be named as follows:

180, 1 *M. hispida* Schldl.
180, 2 *M. discolor* Pers.
180, 3 3 specimens of the *palustris* group
  1 specimen *M. arvensis* (L.) Hill.

Although Linnaeus did not regard these specimens as separate species they belong to species subsequently described by other authors.

The following small-flowered forgetmenots are found in the Netherlands:

M. arvensis (L.) Hill (1764)
M. discolor Pers. (1797)
M. micrantha Pall. ex Lehm. (1817)
M. hispida Schldl. (1814).

The nomenclature of the above-mentioned species, however, is rather confused. In Dutch floras certain synonyms lasted a long time, notably:

instead of *M. arvensis* (L.) Hill: *M. intermedia* Link (1821)
instead of *M. discolor* Pers.: *M. versicolor* (Pers.) Sm. (1797)
instead of *M. micrantha* Pall. ex Lehm.: *M. arenaria* Schrad. (1819)
instead of *M. hispida* Schldl.: *M. collina* Hoffm. (1791).

The name *M. versicolor* has been used until recently by many authors. A. E. WADE revealed in 1952 that "the name *M. versicolor* Sm. (1813, Eng. Bot. sub t. 2558) is antedated by *M. discolor* Pers. (in 1797 Syst. Veg. ed. 15 p. 190 in obs.) which must, therefore, be adopted in its place." G. STROH (1942), however, in his nearly complete list of all synonyms of the species of *Myosotis*, already mentioned *M. discolor* as being synonymous with *M. versicolor* (Pers.) Sm.

The name *M. micrantha* was re-introduced by STROH (1934–'35) when he called attention to LEHMANN (1817) who quoted from the letters of PALLAS.

The epithet *collina* Ehrh. was first used by G. F. HOFFMANN in 1791. It was not clear, however, which taxon was meant. H. G. L. REICHENBACH (1822) was the first to use *M. collina* Ehrh. beside *M. versicolor* Roth. From the description and the quoted synonyms it is evident that Reichenbach's *M. collina* belongs to *M. hispida*. F. C. MERTENS and W. D. J. KOCH (1826) observe, however, that the sample from Ehrhart's Herb. 51 is actually a specimen of *M. discolor*. A. E. WADE is of the same opinion and considers the name *M. collina* a nomen ambiguum (1951), as stated in article 62 of the International Rules of Botanical Nomenclature (1935) (cf. art. 65 Int. Code of Bot. Nom. 1956). Therefore the name *M. collina* cannot be adopted instead of *M. discolor*.

Among the four above-mentioned species, *Myosotis micrantha* Pall. ex Lehm. holds an exceptional place in being rather uniform in its morphological characteristics throughout its distribution. Although a comprehensive treatment of the characteristics is here impossible, a few of them have been selected for discussion. I have attempted to support my taxonomic concepts by carrying out measurements on a few morphological features. It has been known for a long time that the ratio of the length of the lower fruit pedicel to that of the lower fruit calyx is small as compared with the other three species. From measurements it appeared that this ratio lies far below 0.5 and averages 0.26 (50 measurements).

The oblong form of the fruit calyx itself which can be expressed as an index, is also very characteristic (though *M. discolor* approaches this index most).

These two characteristics, combined with the very different hairiness, show an unmistakable difference with those of *M. hispida* (Fig. 1). We emphasize this on purpose because, especially in the Dutch herbaria, these two species: *M. micrantha* and *M. hispida*, especially a form which usually grows on sand dunes but also elsewhere, have

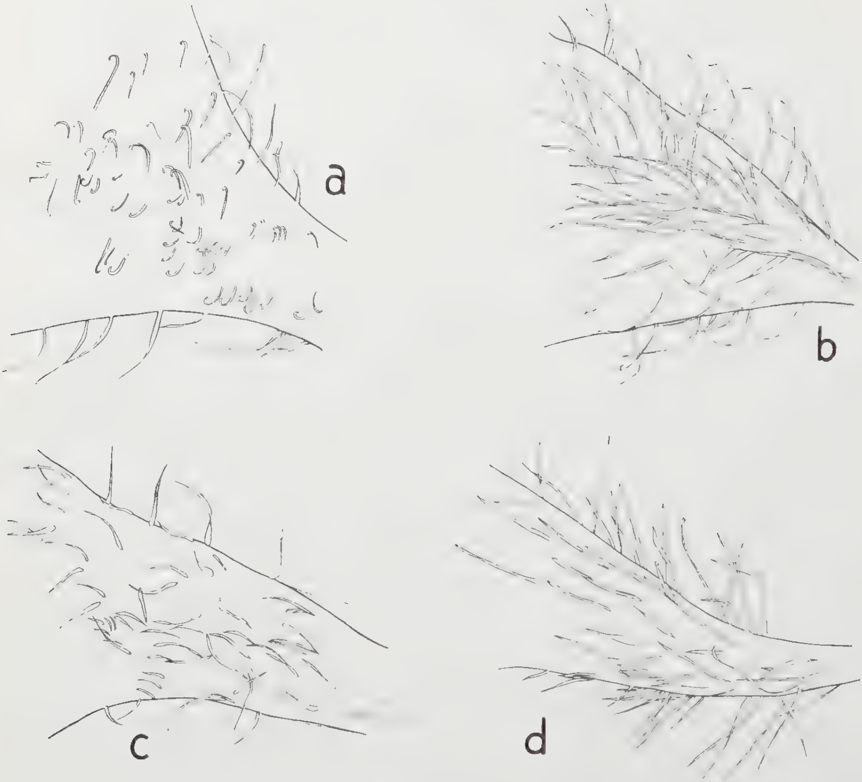


Fig. 1. Hairiness on the under-surface of the leaf—a. *M. micrantha* Pall. ex Lehm.; b. *M. hispida* Schldl.; c. *M. arvensis* (L.) Hill; d. *M. discolor* Pers.

been confused. This form shows a resemblance to *M. hispida* var. *dunensis* Buchenau. Buchenau (1881, p. 100) described it from the West- and East-Frisian Islands, as being characterized by short pedicels and a slender habit. This confusion probably originated because of these short fruit pedicels, although — in my opinion — this dune form is, apart from this, still in other ways different from the typical form of *M. hispida*. The differences in the habit are as follows: The plant is shorter and less leafy; the lower fruit calyx is shorter and the index fruit-pedicel/fruit-aclyx is less than the typical form; the fruit calyx is more closed.

To support my description with exact data, measurements were carried out on several organs of the typical form of *M. hispida* and its "dune form"; likewise of *M. micrantha*. The results were compared and tested according to Wilcoxon (1955). For this purpose the following items come into consideration (each time 50 measurements; Fig. 2):

1. absolute length of lower fruit-calyx (a)
2. index length pedicel/length fruit-calyx (a/b)

3. index width fruit-calyx/length fruit-calyx (c/a). If the calyx was bulging the maximum width was measured., if not then measurement was made half-way the calyx-heigth.
4. index width on top of the fruit calyx/width of fruit calyx (d/c).

Nevertheless, the similarity of the dune form and the typical form is still so evident that no mutual significant differences could be shown concerning points 1 and 3, but concerning points 2 and 4 significance was clear (Figs. 3 and 4). Therefore can be concluded (point 2) that the characterization of Buchenau is still applicable and that (point 4) the fruit calyx of the dune form is more closed.

Differences are to be seen in all the points mentioned between *M. micrantha* and the dune form of *M. hispida.*

Flower measurements have also been carried out. As yet it will only be said that there are significant differences between *M. micrantha* and the dune form, as far as the style length is concerned, and also between the dune form and the typical form. In this respect the dune form is intermediate between *M. micrantha* and the typical form of *M. hispida*, the latter having the longest styles.

Foreign and Dutch material as well as my own field observations indicate a positive correlation between this short form and its habitat: dunes, sandy open grounds, chalk cliffs, etc. This correlation suggests the presence of oecotypes but my experiments on this subject are still in progress.

On the other hand, the few specimens of *M. micrantha* from the Dutch dunes did not show any differences that could suggest a distinct form. The material examined, however, shows that since 1915 *M. micrantha* has no more been found in the dunes. In this respect, no conclusions can yet be drawn.

The existence of a distinct form of *M. arvensis* (L.) Hill is indicated by the Dutch and, to a less extent, by the Norwegian material. This form is characterized by a rigid appearance; the fruit pedicels on one plant do not differ much from each other, and the lower pedicel has an index pedicel/fruit calyx which is much less than that of other *M. arvensis. M. arvensis*, however, has several forms and is variable in such characteristics as foliage, diameter of the corolla, form and proportions of the fruit calyx. Nevertheless, my attention was drawn to the above-mentioned form, because D. Lako, among others, has collected it and classified it as *M. hispida* var. *major* Lako (1916) in M.S.S. He gave the following description of this form in M.S.S.: "Large, well developed plants, with clearly visible inflorescence normally divided into two branches; the upper leaves rounded at the base; calyx teeth rather sharp. Height up to 0.40 m. Flowering-time May–September. Along roads and dikes, on cultivated grounds, on sand and clay soils."

The description as well as the flowering-time and given habitat point to *M. arvensis.*

Lako was not the only one who wanted to classify this form as *M. hispida:* many other collectors were of the same opinion, although

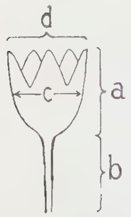
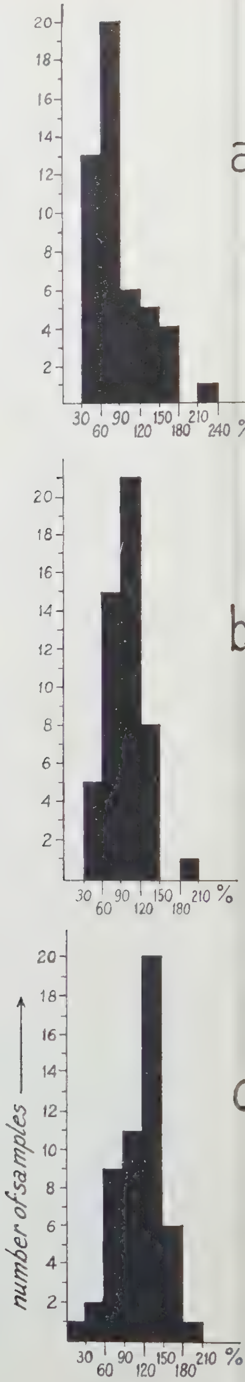


Fig. 2. Scheme.

Fig. 4. Width on top of fruit-calyx/width fruit-calyx—a. *M. micrantha* Pall. ex Lehm.; b. *M. hispida* Schldl., dune form; c. *M. hispida* Schldl., typical form.



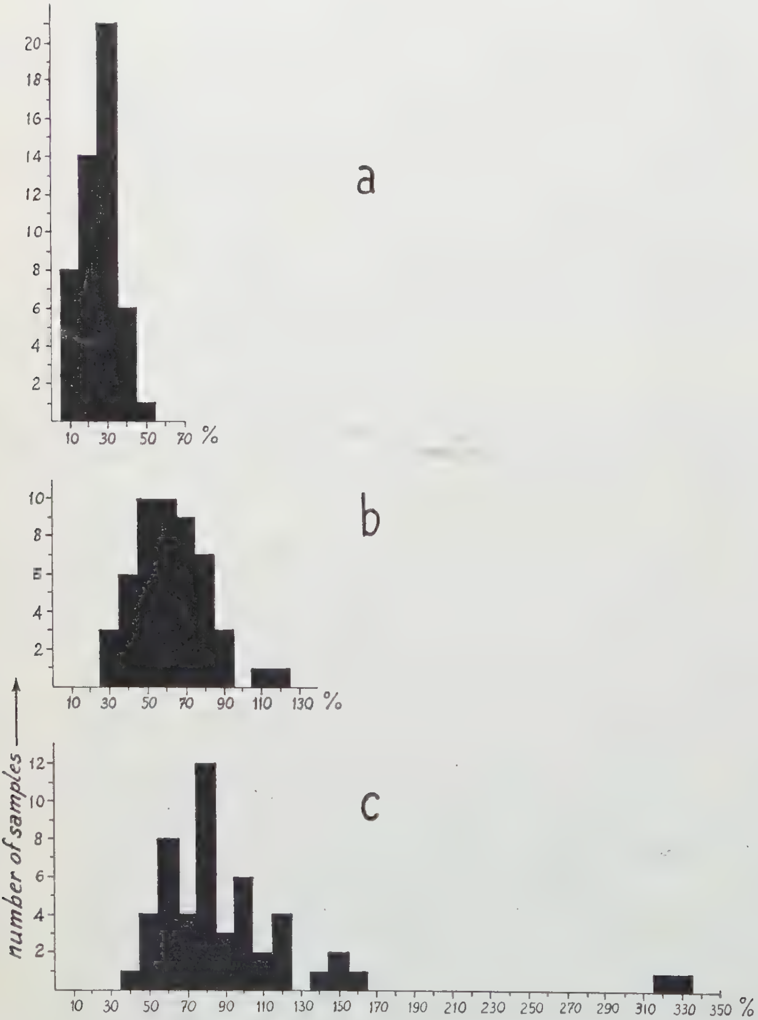


Fig. 3. Fruit-pedicel/fruit-calyx—a. *M. micrantha* Pall. ex Lehm; b. *M. hispida* Schldl., dune form; c. *M. hispida* Schldl. typical form.

perhaps less consciously. In the whole pattern of characteristics, too much value is credited — in my opinion — to the relatively short fruit pedicels. For this reason many felt compelled to classify this form under *M. hispida.* In this way, other characteristics such as size of the plant, foliage and flowering-time were neglected. When these characteristics are analysed mathematically (each time 50 measurements) and tested according to WILCOXON (1955), the index fruit pedicel/fruit-calyx of this form appears to differ significantly from the remaining *M. arvensis* as well as from *M. hispida* (Fig. 5).

Regarding the length of the fruit calyx it is also evident that we are concerned with an intermediate form, the differences being significant. The dimensions of *M.* "*hispida* var. *major*" show more resemblance, however, with those of *M. arvensis.*

The ratio of width and length of fruit calyx showed peculiar results: between *M. arvensis* and *M. hispida* hardly any differences were to be seen. The above-mentioned form, however, shows a lower ratio than the other ones.

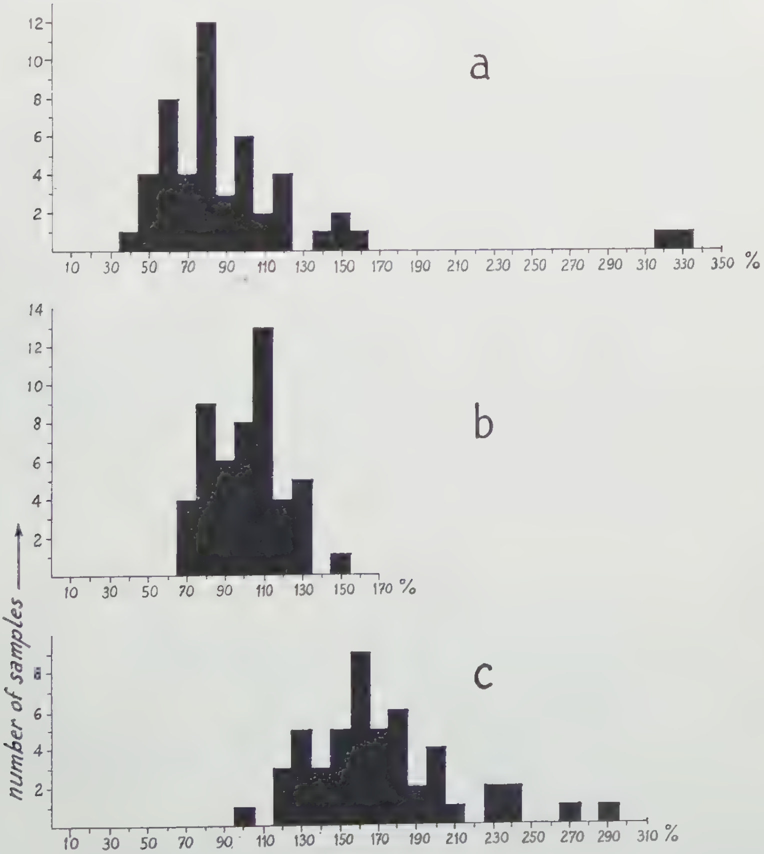


Fig. 5. Fruit-pedicel/fruit-calyx—a. *M. arvensis* (L.) Hill; b. *M. hispida* Schldl. var. *major* Lako; c. *M. hispida* Schldl., typical form.

The flower itself was measured too, but the material was insufficient to give any mathematical support. There are reasons to presume, however, that the form of the flower, the more or less flat corolla lobes and the related indices of corolla tube and total corolla length — which differ notably between *M. hispida* and *M. arvensis* — point to a relationship with *M. arvensis* (Fig. 6).

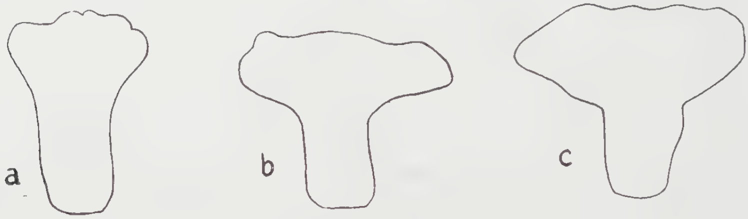


Fig. 6. Corolla shape—a. *M. hispida* Schldl., typical form; b. *M. hispida* Schldl. var. *major* Lako; c. *M. arvensis* (L.) Hill.

Also the hairiness of the plant and the colour and form of the nutlets show more affinity with *M. arvensis* (Fig. 1).

But this form evidently differs from *M. arvensis* with regard to its entire habit and the above-mentioned details. The question arises what taxonomic status should be accorded to it. By studying the literature it appears that many varieties and formae have been created, but that none of these meet the requirements of this form. When reading (e.g. M. J. Cop (1846), E. Zederbauer (1923), A. Chevalier (1941)) that *M. arvensis* shows a seasonal dimorphism and may vary from year to year due to light, soils, humidity, etc., then it is perhaps better to agree with Chevalier who does not identify as to subspecific taxa but describes oecotypes to be expect for different surroundings.

One must not forget that not so many differences appear in the descriptions of these taxa respectively oecotypes but, above all, that the underlying points of view are different.

Unfortunately we cannot, because of a lack of data, relate this form to its habitat.

REFERENCES

Bauhin, C. 1671. Pinax Theatri botanici.
Buchenau, F. 1881. Flora der Ost-Friesischen Inseln: 100.
Chevalier, Aug. 1941. Bull. Mus. Nat. Hist. Nat. 2 sér. **13**: 187.
Cop, M. J. 1846. N. K. A. I, **1**: 466.
Dillenius, J. J. 1719. Catalogus Plantarum Franco Furti.
Hoffmann, G. F. 1791. Deutschl. Flora ed. **1**: 61. Erlangen.
Lehmann, J. G. C. 1817. Beschreibung einiger neuen und wenig bekannten Pflanzen (Asperi Foliae). Halle.
Linnaeus, C. 1753. Species Plantarum.
Lobelius, M. 1655. Stirpium illustrationes. London.
Mertens, F. C. and Koch. W. D. J. 1826. Deurschlands Flora **2**: 48. Frankfurt am Main.
Reichenbach, H. G. L. 1822. Flora Nürnberg.

STROH, G. 1934–'35. Notizblatt des Bot. G. u. Museum Berlin Dahlem **12** no. 114: 471.

————. 1942. Beihefte zum Botanischen Centralblatt. **61** Abt. B: 317.

WADE, A. E. 1951. Watsonia **2**: 107 and 1952: 285.

WILCOXON, F. 1955. Rapport no. S 176 (M 65) Handleiding voor de toets van Wilcoxon door D.r D. Wabeke en C. van Eeden.

ZEDERBAUER, E. 1923. Oesterr. Bot. Zeitschr. **72**: 228.

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THE DIFFERENT STRUCTURE OF THE ROSTELLUM IN OPHRYDEAE AND NEOTTIEAE

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The rostellum in orchids is the organ that forms the viscid liquid which makes it possible for the pollinia to stick to the bodies of visiting insects. The pollinia are then taken along and may be deposited wholly or partly on the stigma of another flower. The rostellum, however, does not occur in all orchids, viz. not in the *Cypripedioideae (Diandrae)*, which do not possess pollinia. It is present in practically all the *Orchioideae (Monandrae)*, on the other hand, but often has very different structures. In the group including *Ophrys*, *Platanthera*, *Habenaria* etc., it forms the viscid discs (viscidia), and in the other groups it usually consists of one single gland (viscidium), such as in *Goodyera*, *Spiranthes* and *Epidendrum*, whereas the simple gland, as we find it in *Vanda* and related genera, is moreover, characterized by a stipes, i.e. a tissue tape of the column formin ghe connection between the viscid disc and the pollinia.

§ 1. THE DIVISION IN THE ORCHIOIDEAE

When gradually a great number of orchids became known and when little by little, the pioneering work of LINDLEY (1853) made it possible to compile a survey of the *Orchidaceae* REICHENBACH (1868) was the first to stress the differences between the *Ophrydeae* (Anthera cum columna connata) on the one hand, where the anther is intergrown with the column, and the *Operculatae* (Anthera demum a columna libera, secedens saltem) on the other hand, in which the anther is completely free or is fixed only at the base (1868 p. 293). PFITZER (1889) distinguished the same two groups, be it under different names, viz. as *Basitonae* versus the *Acrotonae*, according to the place where the viscid liquid comes into contact with the pollinia. With the *Basitonae* (Fig. 1) the viscid liquid is at the base of the vertical or reclining anther, so that the pollinia contact the viscid liquid at their bases. In the great majority of the *Acrotonae* (Fig. 2), on the other hand, the anther is prone and on top of the column, and then the pollinia touch the rostellum with their top and they consequently stick with their top to the viscidia; sometimes there is a stipes between the viscid liquid and the pollinia. The *Basitonae* include only the tribus *Ophrydeae*, whereas the *Acrotonae* consist of the tribus *Neottieae*, *Epidendreae* and *Vandeae*, as they were distinguished by BENTHAM and HOOKER (1883). MANSFELD (1954) made another division, viz. in the contribus *Thrauosphaereae* with loosely constructed pollinia, to which the *Ophrydeae* and the *Neottieae* belong, and the contribus *Kerosphaereae* with the tribus *Epidendreae* and *Vandeae* with waxy or cartilaginous pollinia. It has been found that the *Neottieae*, which, according to Pfitzer, belong to the *Acrotonae-Polychondreae* are not by far all of them acrotonic: some genera, e.g. *Cephalanthera*, have vertical anthers, others are slightly prone, e.g. in the Australian genera *Leptoceras* and *Pterostylis;* in these cases the viscid liquid is deposited in the middle of the pollinia (pleurotonic). Mansfeld, consequently holds that the nature of the pollinia prevails over the attachment of the stamen and the clinging to the viscid discs, in my opinion unjustly, although it is true that in the *Neottieae* there exist all kinds of transitions between basitonic and acrotonic orchids.

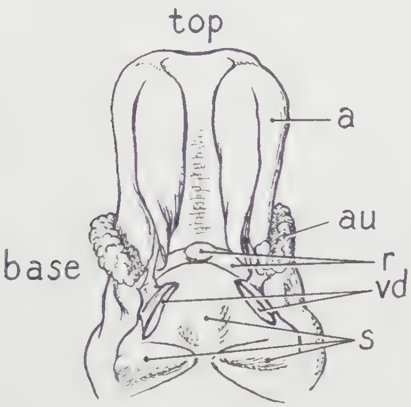

Fig. 1.

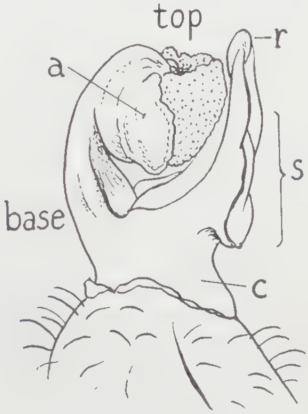

Fig. 2.

Fig. 1. Column of *Platanthera bifolia* (L.) Rich. as an example of a basitonic orchid: the bases of the pollinia are attached to the viscid discs of the rostellum; s: three stigma-lobes; vd: viscid discs; r: tape of the rostellum connecting the viscidia; au: auricle; a: theca of the anther.

Fig. 2. Column of *Goodyera repens* (L.) R. Br. as an example of an acrotonic orchid: the top of the pollinia is attached to the viscid disc (r) of the rostellum; c: column; s: stigma; a: anther; r: rostellum on the backside of which the pollinia are seen (dotted).

§ 2. The rostellum

The rostellum, as a technical term, was first introduced in orchidology by Richard (1818), who defined the term as follows: "Supernus stigmatis processus ultra gynizus (= areo stigmatis viscoso-madida) plerumque ad epicam angustatus . . ." Apparently this definition was inspired by the genus *Orchis* and related genera, where the rostellum is situated between the bases of the thecae (Fig, 3, r), so above the stigma, as a fold with at its base the bursicle, containing the viscidia. In cases where the rostellum does not consist of such a vertical part, it is sometimes hard to recognize. Richard states, that the genus *Platanthera* has no rostellum. Here it is difficult to observe it as a separate organ, but it must be considered as the tissue tape above the stigma, which on either side ends in a viscid disc (plate II, 5 c). For according to the present conception the viscidia should be considered as parts of the rostellum. If RICHARD says that there is no rostellum in *Platanthera*, we apparently have to conclude from it, that there is no distinctly differentiated tissue tape; there are, however, two viscid discs.

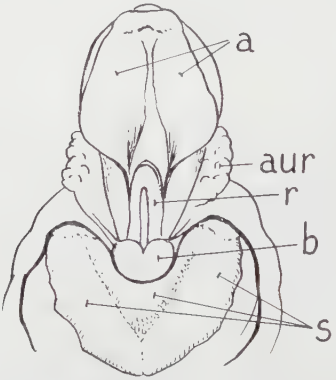

Fig. 3. Column of *Dactylorchis majalis* (Rchb.) Vermln. (= *Orchis latifolia* auct.); s: three stigma-lobes; b: bursicle containing the two viscid discs; r: tape of the rostellum connecting the viscid-discs; aur: auricle; a: two thecae of the anther.

Sometimes, such as in *Orchis*, *Dactylorchis* etc., the viscidia are moreover covered with a bursicle, an enveloping tissue; these bursicles too belong to the rostellum.

In *Epipactis*, *Goodyera* etc., as representatives of the *Neottieae*, the rostellum is much simpler and consists of one single gland centrally situated on top of the stigma. Sometimes this rostellum is a viscid disc, which sticks to visiting insects, sometimes the rostellum forms viscid liquid, which is pressed out on being touched and which ensures the attachment of the pollinia, as in *Listera* and *Neottia*.

§ 3. THE HOMOLOGY OF THE ROSTELLUM. ROBERT BROWN, DARWIN, EICHLER

The first author who occupied himself with the homology of the rostellum was ROBERT BROWN. He mentions the result of his research in 1833, as usual, in very prudently formulated terms. From this it appears that in the opinion of BROWN the viscid discs belong to the median stigma-lobe, though it is not definitely stated that they are homologous with it.

R. BROWN (1833 p. 699) said: "The result of my examination of this point satisfied me that *Orchidaceae* have in reality three stigmata, generally more or less confluent, but in some cases manifestly distinct, and two of which are in several instances even furnished with styles of considerable length" and (p. 701) "In most other cases (in which the lateral stamina are *not* perfect) the anterior lobe, or that placed opposite to the perfect stamen, and deriving its vessels from the same cord, manifestly differs both in form and texture from the other two. To this anterior, or upper lobe, as it generally becomes in the expanded flower, the glands always belong to which the pollen masses become attached, but from which they are in all cases originally distinct, as may be proved even in Ophrydeae."

Lindley (1853) speaks about a gland belonging to the stigma. Considering that Lindley ascribes a small rostellum to the genus *Habenaria*, I wonder which part of this organ the author had in mind.

In 1882 Charles Darwin published the first edition of his splendid work "The various Contrivances by which Orchids are fertilised by insects" and it contains Brown's hypothesis in the extreme form, viz. that the median stigma-lobe has disappeared and has been replaced by the rostellum, in other words, the rostellum is homologous with the median stigma-lobe, which has lost its function as stigma. So in the *Monandrae* or *Orchioideae* there are only two fertile stigma-lobes: the two lateral ones. Darwin said (1890 p. 248): "There is no reason to believe that the whole of this upper stigma, and not merely a part, has been converted into the rostellum; for there are plenty of cases of two stigmas, but not one of three stigmatic surfaces being present in those Orchids which have a rostellum." We find the same hypothesis in the Blütendiagramme by Eichler, and owing to the work of those two brillant scientific workers this became the generally accepted conception of the rostellum, found in all textbooks (Fig. 4).

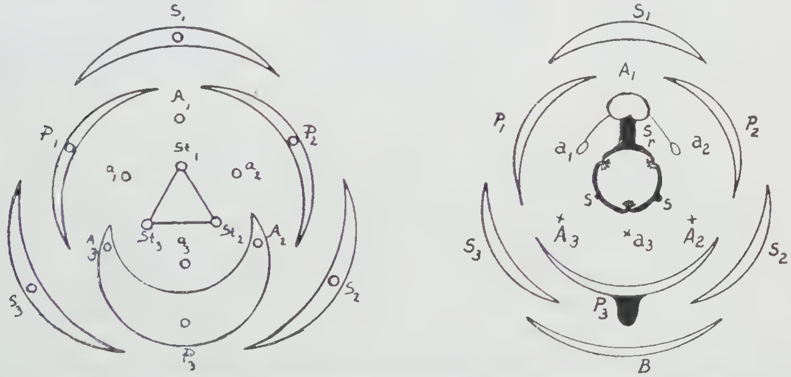

Fig. 4. Floral diagrams of resupinate flowers of the *Orchioideae (Monandrae)*. Left figure by Darwin as suggested by John Lindley; right one by Eichler as suggested by Robert Brown. B: bract; S_1, S_2, S_3: sepals; P_1, P_2: lateral petals; P_3: lip; A_1, A_2, A_3: stamens of the outer whorl; a_1, a_2, a_3: stamens of the inner whorl; s: lateral stigma-lobes; s_r: rostellum; st_1, st_2, st_3: stigma-lobes. In Darwins diagram the stamens A_2 and A_3 of the outer whorl form part of the lip; a_1 and a_2 are staminodes.

§ 4. The homology of the rostellum according to Hagerup

Hagerup (1952, p. 134) posited a different theory; he started from the prototype of the Monocotyledon-flower, which possesses two whorls of three stamens: an outer whorl opposite the sepals and an inner whorl opposite the petals. Hagerup, who examined the flower of

Herminium monorchis (L.) R. Br., was of the opinion that the viscid discs were homologous with the lateral stamens of the outer whorl, while there was, moreover, a gland instead of the median stigma-lobe: so there would be "two different kinds of viscid organs". In *Dactylorchis maculata* (L.) Vermln (= *Orchis maculatus* L.) he considered the bursicle homologous with the two lateral outer stamens and the auricles with the two lateral inner stamens. Hagerup is therefore trying to find an explanation for the two glands of the Ophrydeae. (Fig. 5).

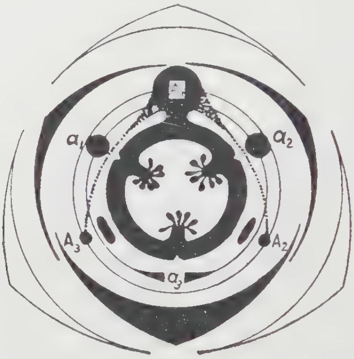

Fig. 5. Floral diagram of a resupinate flower of *Herminium* as suggested by Hagerup. A_2 and A_3 form the viscid discs; a_1 and a_2 are staminodes; A_1 is the fertile stamen.

§ 5. Criticism of hagerup's theory

Two arguments may be advanced against this theory:

1. If it were true that the viscid discs resp. the bursicle of *Herminium*, *Orchis*, *Dactylorchis*, etc. are homologous with the outer stamens, the latter would lie more inwards than the auricles, which correspond with the inner stamens, since they lie nearer to the stigma, which forms the centre of the flower. In this case these organs would have been transposed, which seems very unlikely.

2. The theory does not take into consideration the remarkable zygomorphy of the orchid flower. In some families of the *Monocotyledoneae* there is a tendency to keep three of the six stamens fertile, viz. those turned away from the axis in their bud-stage, consequently the three ventral ones: the median one of the outer whorl and the two lateral ones of the inner whorl; the three dorsal ones either become smaller or sterile or they disappear altogether. This tendency is apparent in the *Commelinaceae*, in the *Pontederiaceae*, in the *Apostasiaceae* and finally, in the most extreme form, in the *Orchidaceae*. The *Commelinaceae* show all the transitions between six fertile stamens and three dorsal sterile and three ventral fertile stamens. Some genera of the *Pontederiaceae* have three long and three shorter stamens as a result of their trimorphy, but there too, the dorsal ones are unlike the ventral ones. The *Apostasiaceae* have only the ventral stamens developed, the others have completely disappeared. This is seen best in *Nieuwedia* (plate I, 1a & 1b), where all three ventral stamens are fertile. In the genus

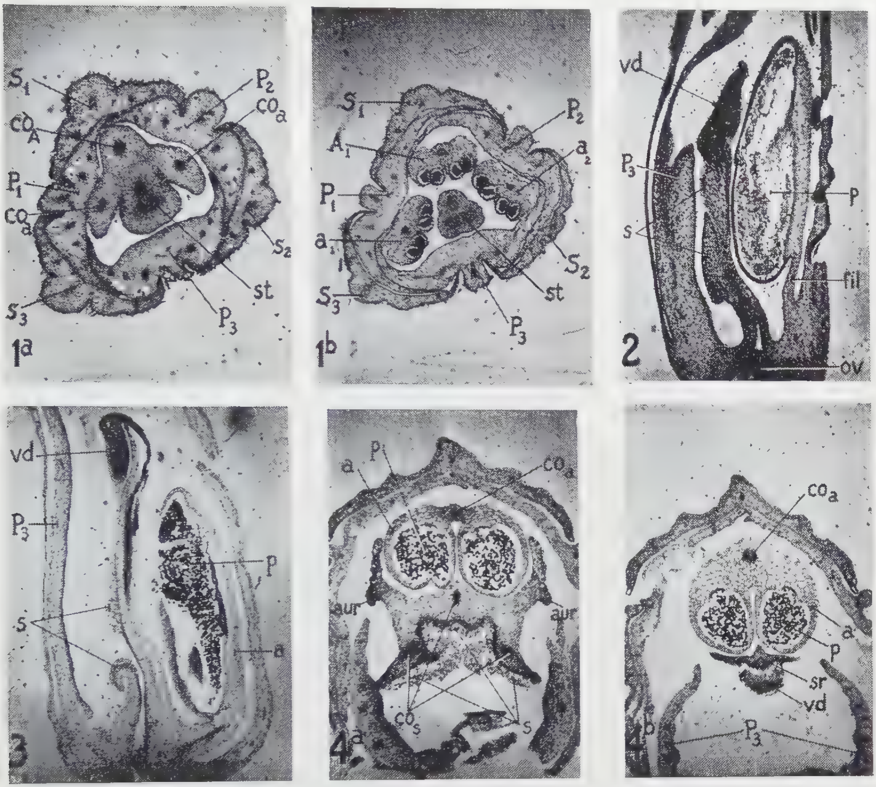

Plate I. 1a and 1b: Cross sections through the flower of *Neuwiedia veratrifolia* Blume; 1a: lower one with column; 1b: higher one with style and three anthers; 2: longitudinal section of flower of *Diuris semilunulata* Messmer; 3: id. of *Prasophyllum elatum* R. Br., the viscid disc has a long thread; 4a and 4b: cross sections of flower of *Epipactis helleborine* (Mill.) Crantz; 4a with three stigma-lobes; 4b with median lobe and viscid disc. a: anther; A_1: anther of the outer whorl; a_1 and a_2: lateral anthers of the inner whorl; co_A: vascular cord of anther A_1; co_a: vascular cord of anthers a_1 and a_2; co_s vascular cords (3) of stigma; fil: filament; ov: ovary; P_1, P_2: lateral petals; P_3: median petal or lip; p: pollen; S_1, S_2, S_3: sepals; s: stigma-lobes (3); s_r: third or median stigma-lobe; st: style with vascular cords (3); vd: viscid disc.

Apostasia we find a condition which may be compared with that of the *Cypripedioideae:* of the three ventral stamens the two lateral ones of the inner whorl are fertile, the median one of the outer whorl is sterile. In the *Orchioideae* only the median ventral stamen of the outer whorl is fertile; the lateral stamens have either disappeared altogether or they have remained only as staminodes.

One sometimes wonders if perhaps in the *Ophrydeae* this state has developed from a flower with only three outer stamens (as in the *Iridaceae);* in that case the median stamen would remain if there were a tendency to promote the ventral part of the androecium. In my opinion an argument for this theory is that if there is an extra stamen, as happens sometimes, it is always a lateral one of the outer whorl.

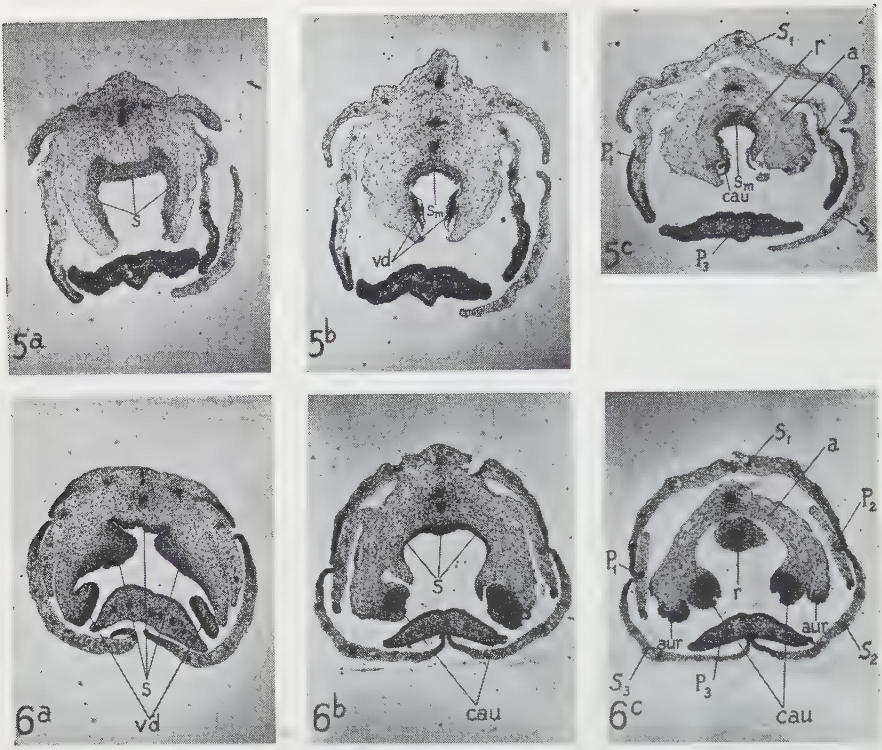

Plate II. 5: Three cross sections of a flowerbud of *Platanthera bifolia* (L.) Rich. 5a: lowest section with three stigma-lobes; 5b: somewhat higher with viscid discs on the place of the lateral stigma-lobes, third stigma-lobe still present; 5c: still higher, rostellum separated from the anther and still with the third stigma-lobe. 6: Three cross sections of a flowerbud of *Platanthera chloranha* (Cust.) Rchb. 6a lowest section: column with three stigma-lobes and viscid discs at the end of the lateral lobes; 6b higher section showing caudicles separated from the stigma tissue; 6c still higher with rostellum and anther with auricles and caudicles. a: anther; aur: auricle; cau: caudicle; P_1, P_2: lateral petals; P_3: lip; r: rostellum with top of median stigma-lobe (s_m); s: stigma-lobes; s_m; median stigma-lobe; S_1, S_2, S_3: sepals; vd: viscid discs.

If the conception of zygomorphy, as here presented, is true, it seems extremely unlikely that the lateral (dorsal) stamens off the outer whorl should develop as viscid discs.

The order of the *Zingiberales* differs from the families mentioned, in that of the two whorls of stamens all the four lateral ones are either fertile or staminodes; one of the median stamens is usually sterile and one fertile, but the tendency: promotion of the ventral opposite the dorsal ones *in both whorls* is lacking.

§ 6. Criticism of darwin-eichler's hypothesis

If the hypothesis of Darwin-Eichler were true, the *Orchioideae* or *Monandrae* would include no species, which possess three stigma-lobes, since the median stigma-lobe has become a rostellum. In my previous article, The Rostellum of the Ophrydeae (1955), I showed, however, by means of photographs of sections of flowerbuds of the genera *Orchis*, *Galeorchis*, *Ophrys* and *Himantoglossum*, that these have indeed three stigma-lobes. This also applies to the genera *Dactylorchis*, *Coeloglossum* and *Platanthera* and several more. Moreover all these genera possess a rostellum, which proves therefore, that rostellum and third stigma-lobe cannot possibly be homologous. The rostellum, I argued, must be considered as a new organ, which is characteristic of the *Orchioideae*, just as the corona is a new organ for the *Asclepiadaceae*. It is remarkable that in the two families where a new organ has appeared, there are also pollinia, and small transport organs, retinacula and translators resp., are developed.

§ 7. SERIES OF DEVELOPMENTS OF THE ROSTELLUM ACCORDING TO DARWIN

In Chapter IX of his book, under "Gradation of Organs", DARWIN (1890) deals with a series of developments from *Anacamptis* with only one single viscid disc to *Coeloglossum viride* (L.) Hartm. (= *Platanthera viridis* (L.) Lindl. = *Habenaria viridis* (L.) R. Br. = *Peristylus viridis* (L.) Lindl.) with two separate discs, connected by a roof-shaped tape of the rostellum (Fig. 6). DARWIN then says: "These facts are intelligible only on the view, that, whilst the two discs were gradually brought together, during a long series of generations, the intermediate portion or summit of the rostellum became more and more arched, until a folded crest, and finally a solid ridge was formed" (DARWIN, 1890 p. 256). I completely agree with this view of Darwin's. The development of bursicles particularly in the genera with a folded crest is another indication of the truth of the conception that this state is a derived one and not primitive.

It is then obvious to assume, however, that the roof-shaped tape is not the most primitive state, but that we should look for this among those genera where this tape is almost straight and lies immediately above the stigma. I think I have found an example of this in the genus *Platanthera*. In some species of that genus, which is distinguished from *Habenaria* in that the stigma forms a whole, has three lobes and not two, both thecae diverge considerably and the connective is very broad, as in *P. chlorantha* (Cust.) Rchb., *P. hookeri* Torr. ex Gray and *P. orbiculata* (Pursh) Torr. (the latter two are American species); this state must be considered as derivative. The European species *P. bifolia*, on the other hand, has a practically normal connective and, here, where the rostellum does not form an arched ridge above the stigma, I suppose to have found a primitive species. *P. blumei* Lindl. from Indonesia has already a somewhat diverging connective but a primitive rostellum as shown in fig. 11.

§ 8. TWO SERIES OF DEVELOPMENT

In the genus *Platanthera* we find a rostellum consisting of a narrow tissue tape above the stigma, with on either side a terminal naked viscid disc (plate II, 5). In *P. bifolia* the viscid discs lie quite near and opposite each other, at the foot of the thecae at the end of the caudicles of the pollinia. In the frogorchid *(Coeloglossum viride = Peristylus viridis* , which distinctly possesses three stigma-lobes (See Schlechter, 1928 Tafel 30 nr. 117 and Vermeulen, 1958 I, 5 fig. 22 p. 49) the rostellum begins to detach itself from the stigma so to say: the rostellum takes on a roof-shape and the viscidia get a little closer to each other (Fig. 6). In *Herminium* the tape of the rostellum has the shape of a horse-shoe. In the genera *Gymnadenia* and *Nigritella* the arching has developed to such an extent that both halves of the tape have come so near to each other that there remains only a narrow interstice in between, which shows how this crest has come about.

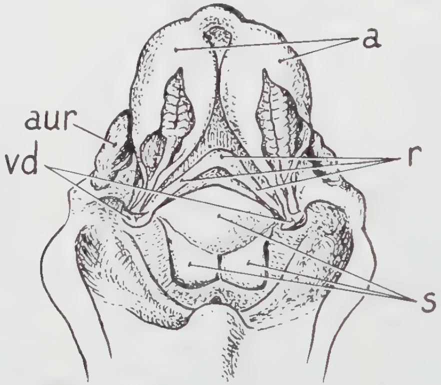

Fig. 6. Column of *Coeloglossum viride* (L.) Hartm. (= *Peristylus viridis* (L.) Lindl.); s: three stigma-lobes; vd: viscid discs; r: tape of the rostellum connecting the viscid discs; aur: auricle; a: thecae of the anther.

Richard (1818) speaks of a "rostellum fissum". We find a similar rostellum in *Orchis*, *Dactylorchis* (Fig. 3), *Galeorchis*, but here a bursicle has developed around the viscidia. In the genus *Anacamptis* the viscid discs are connate and ringshaped and both halves of the tape of the rostellum have become a simple ridge between the thecae. This genus forms the end of the series on the one side. For the series on the other side, we can start again with *Platanthera*, but now with *P. chlorantha:* here the connective has become broad and the thecae are separated from each other. The viscid discs lie at the ends of the caudicles of the pollinia: so the rostellum has become longer. We find a similar state in *Blephariglottis ciliaris* (L.) Rydb. (= *Habenaria ciliaris* (L.) R. Br.) from North America, but here the ends of the two thecae project from the column. The tendency of the thecae to become longer also communicates itself to the arms of the rostellum, which is necessary to bring the two viscidia near the ends of the caudicles. We see a similar symptom in the genus *Pecteilis*, e.g. in *P. susannae* (L.) Raf. (= *Platanthera susannae* (L.) Lindl. = *Habenaria susannae* (L.) R. Br.) from Indonesia. In the genera *Blephariglottis* and *Pecteilis* the stigma has remained simple, i.e. it has three lobes. In the genus *Habenaria* sensu stricto there are two stigma-lobes in which, in some species, have hardly become longer, but which, in other species, have clearly developed into separate stigmaphores. The median stigma-lobe has not been developed. In the species *Habenaria arietina* Hook. f. the projecting parts of the thecae are very long, but the ends approach each other very closely, just as the ends of the rostellum and the two viscid discs, so that a visiting insect will easily take along both pollinia. We find a similar state in the South African genus *Bonatea* (Fig. 7 en 8); here there are also two long stigmaphores; the rostellum has become crest-shaped (this crest is perhaps part of the *receptacle* grown upwards) and completely clear of the anther, but yet the two rostellum arms develop to such an extend that the viscid discs come to lie near the end of the caudicles of the pollinia.

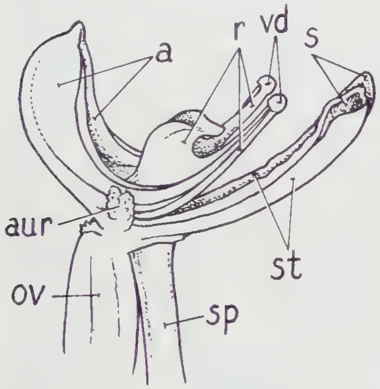

Fig. 7.

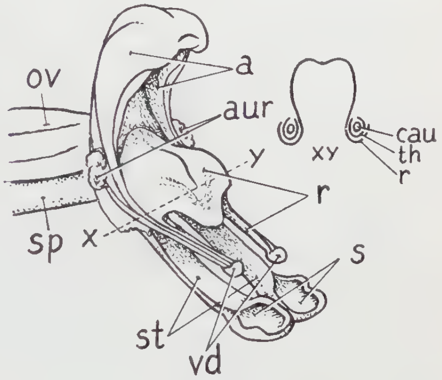

Fig. 8.

Fig. 7. Side view of the column of *Bonatea speciosa* (L. f.) Willd.; ov: ovary; sp: spur of the lip; st: stigmaphores; s: two stigma-lobes; vd: viscid discs; r: parts of the rostellum; aur: auricle; a: thecae of the anther.

Fig. 8. Column of *Bonatea speciosa* (L. f.) Willd. seen slantingly from above; the letters are the same as in fig. 7. The small figure on the right gives a cross section through line x-y; r: rostellum; th: theca; cau: caudicle of the pollinium.

In the genus *Platanthera* the rostellum completely surrounds the upper part of the stigma. In other genera, however, on the one hand the rostellum detaches itself entirely and forms a fold, the two discs intergrowing, on the other hand the arms of the rostellum become considerably longer, and finally approach each other, because of which the viscidia also come to lie near each other.

§ 9. OPHRYDEAE OF THE SOUTHERN HEMISPHERE. THEIR ROSTELLUM

South Africa is a centre for the development of the *Ophrydeae* in the Southern Hemisphere. Here we find the genus *Disa* with more than a hundred species, which is characterized by a distinct three-lobed stigma. BOLUS (1918 p. 67 and p. 68), who accepts DARWIN's theory, nevertheless mentions that in *Disa maculata* L. f. and in *Disa uniflora* Berg. the stigma is three-lobed. The most striking feature of the column in this genus is that the stigma is indeed right above the ovary, so that the rest of the column must consist of the receptacle with the anther; otherwise we should have to assume that the column above the stigma were the filament; usually the rostellum is a more or less *curved tape* here, but clearly separated from the stigma. In some species, however, there is only one viscidium (sections *Monadenia* & *Herschelia* – LINDLEY considered these two as separate genera).

In the genus *Satyrium* the flower is not resupinate and the labellum, bearing two spurs, is turned upwards. The column splits in two parts at the top, one part bearing the stigma, the other part, turned downwards, is considered to be the rostellum (Fig. 9); it bears two viscidia at the sides, with which the caudicles combine. Here the anther is reclined, so that the dorsal part touches the column. Because of this remarkable structure of the column *torsion* of the flower is not necessary to make pollination possible all the same. In the species *Satyrium ryncanthum* Bolus the two viscid discs have intergrown again and the rostellum is very small.

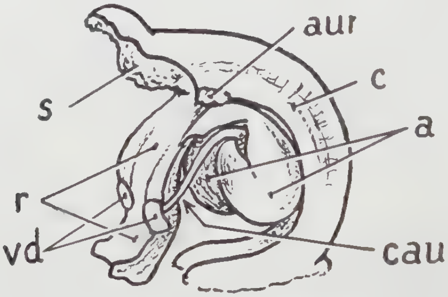

Fig. 9. Side view of the column of *Satyrium nepalense* Don; vd: viscid discs; r: rostellum; s: stigma; aur: auricle; c: column; a: thecae of the anther; cau: caudicle of the pollinium.

In the genus *Holothrix* there is only one viscid disc, but it seems as if here the whole rostellum is taken along, for between the places where the pollinia are connected there is a projecting part, corresponding with the "crest" in *Anacamptis*. Also in the other South African genera *Pterygodium*, *Ceratandra*, *Disperis*, it gives the impression that again and again the rostellum is a crest with the viscidia at the ends; where there is only one viscid disc, this seems a derived condition. In these last mentioned genera, one also finds — just as in *Habenaria* s.s. — two distinct stigma-lobes. Apart from *Satyrium* there is a similar condition in the South African genera as in the Northern Hemisphere ones: a rostellum consisting of a tissue tape with two viscid discs at the ends.

§ 10. THE ROSTELLUM IN THE NEOTTIEAE

The rostellum in the *Neottieae* is completely different. Here is no question of a tissue tape nor of two viscid discs. On the contrary, here the rostellum, the organ producing the viscid liquid, consists of one simple gland. In the most primitive representatives of the tribus, e.g. in the genus *Cephalanthera*, the rostellum is lacking; perhaps the upper ridge of the stigma, rich in viscid liquid, may be regarded as a rostellum. The stigma here is very rich in viscid liquid and with the help of this sticky secretion the pollinia are indeed stuck to the visiting insects. So this is apparently a primitive state. In the related genus *Epipactis* we find a number of species which possess a rostellum, lying in the middle above the median stigma-lobe and which looks like a simple gland. In some *Epipactis*-species, however, there seems to be no rostellum, e.g. in *E. leptochila* (Godf.) Godf., *E. muelleri* Godf., *E. confusa* Young etc., and one wonders whether here we have to deal with a case of reduction or with a primitive state reminiscent of *Cephalanthera*. The latter does not seem excluded.

A rostellum consisting of one simple gland is indeed the ordinary state in the *Neottieae*, both in the genera of the Northern and the Southern Hemisphere. *Goodyera*, *Spiranthes*, *Diuris* (plate I, 2), *Glossodia*, *Thelymitra*, *Caladenia* etc. always show a simple rostellum. In the Australian genus *Prasophyllum* the rostellum is very long and a thin thread forms the connection between the gland and the pollinia (pl. I, 3); in *Acianthus* it gives the impression that the rostellum is split (Rupp, 1943). In general, however, these appear to be exceptions. Sometimes the gland lies right above the stigma, but in *Goodyera* (Fig. 2) the gland is fitted in between two teeth, distinctly separated from the stigma. The teeth remain when the gland with the two pollinia is removed. In all these genera the stigma always forms a whole; because of the mucus, which more or less covers the stigma, it is hard to ascertain whether there are two or three lobes. I think that there are sometimes three, as in *Cephalanthera*, *Epipactis*, *Spiranthes*. Were there is no distinct separation between the stigma and the viscid disc, it seems as if the disc is more or less a continuation of the stigma, often only separated from it by means of a slight interruption (plate I, 4b). In *Listera* and related genera the rostellum consists of partitions, from which, when touched, viscid liquid is pressed out.

§ 11. The vascular cords in the column

Darwin gives an accurate description of the number of the vascular cords in the column of several orchids (1890, p. 239 note etc.).

In the *Neottieae* we often find at the column small projecting parts, which are looked upon as staminodes. In most cases they contain no vascular cords and the supposition that we have to do with remnants of the lateral stamina of the inner whorl cannot be proved. In some genera, however, the lateral projecting parts are large, as in the Australian genera *Pterostylis*, *Diuris*, where the anther lies apart from the rest of the column (plate I, 2), *Caladenia* and *Thelymitra*, and they form wings at the column. It appears that these projecting parts contain vascular cords, which arise from the cords of the lateral petals, in which case they would be homologous with the lateral stamina of the inner whorl. Besides the vascular cords for the stamen and staminodes the column usually contains three cords. These cords are found opposite the sepals. The median cord, which also provides for the rostellum, is well developed, apparently in connection with the double task which the cord has to fulfill.

In the *Ophrydeae* the gynostemium often has only one single vascular cord, which lies in front of that of the median sepal. This cord splits into two parts: one branch enters the connective and provides for the anther; the other branch apparently has to cater for the rest of the column and usually this branch leads to the rostellum. If the rostellum is broad as in *Platanthera chlorantha*, there yet remains one simple and that is the median vascular cord. I consider this state (one vascular cord) as a derived one, that of the *Neottieae* (three vascular cords) as more primitive.

In *Habenaria arietina* with two long stigmaphores, each of these also contains a vascular cord. (Is this also the case with *Bonatea?)*. An exception is the genus *Satyrium* from Africa, with one single species, *S. nepalense* Don., occurring as far north as in the Himalayas. Here we find a long column, containing three vascular cords, of which the median one again provides for the rostellum and the stigma. Wether the same is the case in the other South African genera, I have not been able to investigate.

In the *Ophrydeae* the anther nearly always has auricles, which Brown, Darwin and Eichler consider to be staminodes. Brown (1833), however, is in doubt, because in a flower of a *Platanthera*, which had an extra stamen, the latter also had an auricle at the side of the median, normal stamen. I have found a similar case in *Dactylorchis maculata*. These auricles are in my opinion to be considered as appendices of the stamen, as they are also found in the stamens of *Allium* (see my article "The vanished stamens" (1953)). In the *Ophrydeae* these auricles always contain raphides. They never have a vascular cord. The *Neottieae* have more often staminodes but *Epipactis* (plate I, 4) and *Cephalanthera* have auricles.

§ 12. THE DIFFERENCES BETWEEN OPHRYDEAE AND NEOTTIEAE

Comparing these two tribes, we find the following differences in the column:

OPHRYDEAE	NEOTTIEAE
Anther intergrown with its backside with the column.	Anther connected with a broad base or only by means of the filament with the column.
Column with anther with auricles, no staminodes.	Column often with wings, which are probably staminodes; anther seldom with auricles.
Pollinia with caudicles at their bases and basitonic.	Pollinia never with caudicles; pollinia pleurotonic or acrotonic.
Rostellum more or less in the shape of a tape with a viscid disc on either end; sometimes one or two bursicles.	Rostellum a simple viscid disc above the median stigma-lobe, consisting only of viscid matter or of a gland, forming viscid liquid, never bursicles.
Stigma one whole, with three lobes, or stigma with two separate lobes.	Stigma more or less clearly provided with three lobes or with two lobes, which always form a whole.

Besides other differences especially the one in the structure of the rostellum is apparent. DARWIN concluded that the rostellum in the *Ophrydeae* was originally an organ with two viscid discs. Gradually a simple rostellum may have developed from this. In the §§ 8, 9 and 10 I have tried to prove that these differences between the rostellum of *Ophrydeae* and *Neottieae* are essential and not accidental. How is one to imagine the original state in the *Ophrydeae?*

§ 13. EPIPACTIS GIGANTEA DOUGL. EX HOOK

Accidentally my attention was drawn by the gynostemium of *Epipactis gigantea* Dougl. ex Hook., which was blossoming in the Amsterdam Hortus Botanicus in 1958. This species, which has a movable epichilium at the hypochilium, like *E. palustris* (Mill.) Crantz, shows a peculiarity. For this point I have consulted CORRELL's book "Native Orchids of North America", 1950, page 129 of which gives a reproduction of this species. The column, however, is not reproduced. Also in the case of *Habenaria* Correll's book continually fails us. The American authors take as general a view of this genus as do BENTHAM and HOOKER (1883), but they do not pay attention to the structure of the column, consequently they neither deal with the peculiarities of the stigma, nor with that of the rostellum. It is true that the structure of the perigone, in particular that of the labellum, is sufficient to determine the name of the species, but this does not give us sufficient insight into the relationship between the species, and that should be considered as one of the most important aims of systematics.

The gynostemium of *E. gigantea* shows a stigma with three lobes, and near or above these lobes three spots occur, which secrete viscid matter. Most viscid liquid is above the median lobe, close below the

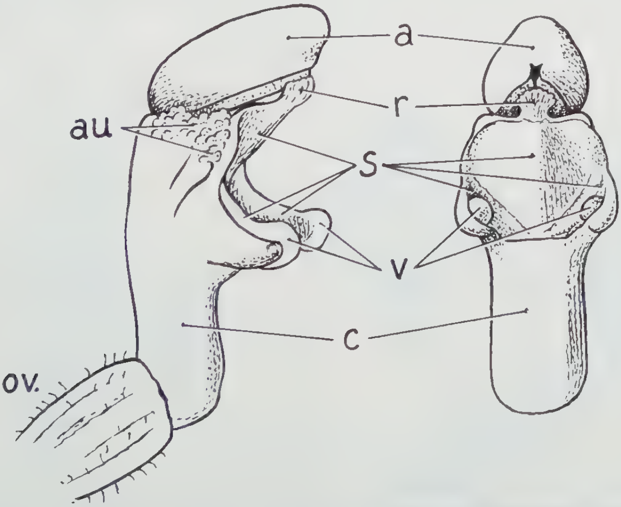

Fig. 10. Side view (left) and front view of the column of *Epipactis gigantea* Dougl. ex Hook.; ov: ovary; c: column; v: sticking fluid on the side lobes of the stigma; s: three stigma-lobes; aur: auricle; r: rostellum; a: anther.

top of the anther and it is this which forms the rostellum. There is only a slight separation between the median stigma-lobe and this rostellum. With the help of the viscid liquid, formed by this small organ, the pollinia are stuck with their tops to the head of a visiting insect. The organ forming this viscid fluid is simple, as is always the case in the *Neottieae*. The two other spots forming viscid liquid are on short arms on the lateral stigma-lobes (Fig. 10). It does not seem probable that this viscid fluid plays a part in the transportation of the pollinia. In this connection it appears important to me, however, that not only above the median stigma-lobe a gland with viscid fluid can be formed, but that it seems probable that such glands can also arise above the lateral stigma-lobes. It seems important that this ability to form lateral glands is formed in the genus *Epipactis*, which shows primitive properties also in another respect: a rostellum is lacking in some species.

§ 14. THE ROSTELLUM IN PLATANTHERA BIFOLIA (L.) RICH

The fact that viscid fluid is secreted also through the lateral lobes of the stigma in *Epipactis gigantea* suggested the idea to me that the two viscid discs of the *Ophrydeae* might have arisen or formed by and above the lateral stigma-lobes, whereas in this group viscid liquid would not be formed by or above the median stigma-lobe. If this thought should contain a substratum of truth, this state would have to be verified in primitive *Ophrydeae*, consequently in such species where the rostellum still lies above and against the stigma, and is not or hardly differentiated, such as in the genus *Platanthera*. Then the species with hardly broadened connective, *P. bifolia*, would have to show this the most clearly. A cross-section of the gynostemium has three distinct stigma-lobes (plate II, 5a). Indeed, the viscid discs answer the expectation; just as the viscid disc in *Epipactis* lays above the median stigma-lobe, in the same way the two viscid discs of *P.*

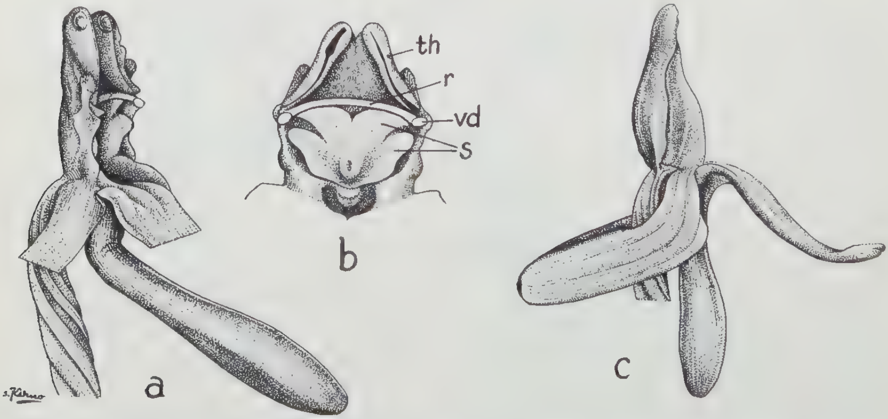

Fig. 11. *Platanthera blumei* Lindl. c: flower; a: flower without sepals and lateral petals, the lamina of the lip is cut away; b: column with; s: stigma; vd: viscid disc; r: tape of the rostellum; th: theca of the anther.

bifolia lay right above the lateral stigma-lobes and with *P. blumei* it is the same (Fig. 11).

In *P. chlorantha*, where the connective is already broadened considerably, the viscid discs lie beside the lateral stigma-lobes (plate II, 6a). If in these three *Platanthera* species, we speak of a rostellum, we can regard the two viscid discs as such and we can speak of a separate tissue tape, which connects them (plate II, 5c, 6c). It is true that the tissue on which the stigma is situated, continues for a small distance and there is even a separation between this tissue and the stamen. In my opinion this tape must be regarded as the primitive origin of the connecting tape between the viscidia, which, in other genera, forms an integral part of the rostellum.

§ 15. Gradation of the rostellum. criticism of brown

The rostellum would consequently have developed from this primitive organ, hardly to be distinguished, into a separate tissue tape, which appears to be a separate organ. In one series there seem to be a tendency to detach this organ from the stigma. In *Coeloglossum* it can be distinguished as a roof-shaped ridge with at the ends the viscidia, which have approached each other but they are still in connection with and lying above the lateral stigma-lobes (Fig. 6). In *Herminium* the connecting tape is curved in the shape of a horse-shoe; in *Galeorchis* and *Ophrys* the two halves come closer until finally both touch each other in the genera *Gymnadenia*, *Orchis*, *Dactylorchis* (Fig. 3) etc. In the other series *(Pecteilis, Habenaria, Bonatea)* the connecting ridge between the viscid discs shows the tendency to lengthen and the viscidia are more separated; there is no question of a rising ridge. Both ends of the rostellum keep pace with the lengthening of the thecae, as a result of which the viscid discs always remain at the ends of the pollinia (Fig. 7 & 8).

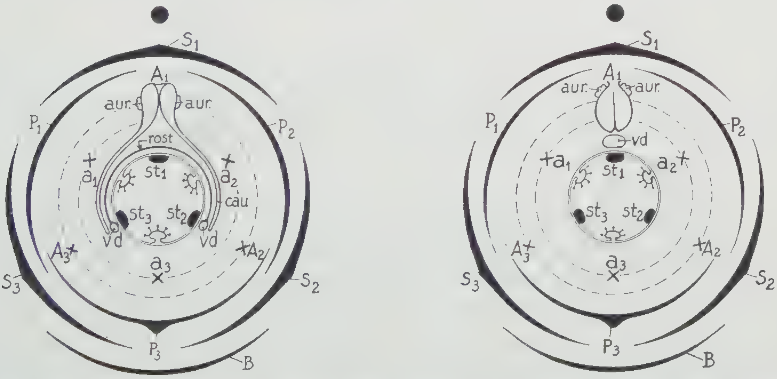

Fig. 12. Floral diagrams of *Platanthera bifolia* (L.) Rich. (left) and *Epipactis helleborine* (Mill.) Crantz (right) as suggested by the author. B: bract; S: sepals; P: petals (P_3: lip); A_1: fertile stamen of the outer whorl with aur: auricle and cau: caudicle; A_2 and A_3: place of the lateral outer stamens which are suppressed; $_1a$, a_2, a_3: stamens of the inner whorl which are all suppressed; rost: rostellum; vd: viscid discs of it; st_1, st_2, st_3: fertile stigma-lobes. Flowers resupinate.

In several genera of the *Ophrydeae* there is a tendency to reduce the median stigma-lobe so as in *Gymnadenia* and *Anacamptis* (Vermeulen, 1958 p. 31 fig. 10, 4 and p. 51 fig. 23, 5). This lobe is situated opposite the anther which is normal. In *Habenaria* s.s., *Bonatea* and several other South African genera the third stigma-lobe has totally disappeared, whereas the thecae of the anther are more or less lengthened at their base. The rostellum ridge is lengthened in the same way. This may be an indication the more that the ridge does not belong to the third lobe but behaves as an independant organ (Vermeulen, 1954). Sometimes the middle part of the rostellum becomes very broad as in *Bonatea, Cynorchis, Platycorne* etc. All these cases seem to be derived and it is impossible to establish here if the viscid discs originally are situated above and near the lateral stigma-lobes. Therefore it is necessary to look for primitive genera like *Platanthera*. However, it must be possible to verify the original state of the rostellum with other primitive genera in the *Ophrydeae* too.

The hypothesis: the glands in the *Ophrydeae* are originally formed near and in contact with the lateral stigma-lobes, is contrary to the hypothesis, which Robert Brown posed in 1833, viz. that the glands would always belong to the upper lobe of the stigma. Fig. 12 gives the differences between *Platanthera* and *Epipactis* in diagrams.

§ 16. CONCLUSIONS

From the foregoing I think I may draw the following conclusions:

1. There is an essential difference between the rostellum in the *Ophrydeae* and the *Neottieae*.
2. In the *Ophrydeae* it consists of a tape or ridge with a viscid disc at each of its ends.
3. In the *Neottieae* the rostellum consists of a simple organ.
4. In many *Ophrydeae* the stigma has three lobes. Several *Neottieae* too have a stigma with three lobes. This is contrary the opinion of Darwin and Eichler.
5. Near and on all three stigma-lobes of *Epipactis gigantea* Dougl. ex Hook. a small organ develops, forming viscid liquid. I suppose that from a similar state as starting-point the development of the rostellum evolved in two directions: one leading to the *Neottieae* and the other to the *Ophrydeae*.
6. In the *Neottieae* with three stigmata it seems as if the rostellum has been formed in connection with or above the *median* stigma-lobe.
7. In the primitive genera of the *Ophrydeae*, however, both viscid discs appear to originate in connection with or above the lateral stigma-lobes. This is contrary the opinion which Robert Brown posed in 1833.
8. In the derived forms of the *Ophrydeae* the connection between the viscid discs and the lateral stigma-lobes may be completely broken. This is to be described to the independent development which the rostellum, as a new organ, can apparently go through.

ACKNOWLEDGEMENTS

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REFERENCES

Bentham & Hooker. 1883. Genera Plantarum **3**.
Bolus, Harry. 1918. The Orchids of the Cape Peninsula. Cape Town.
Brown, R. 1833. Observations on the organs and mode of fecundation in the Orchideae and Asclepiadeae. Transact. Linn. Soc. **16**.
Correll, Donavan Stewert. 1950. Native Orchids of North America north of Mexico. Waltham, Mass.
Darwin, Charles. 1890. The various contrivances by which Orchids are fertilised by Insects. 2nd ed. London.
Eichler, A. W. 1875. Blüthendiagramme. 1. Theil. Leipzig.
Hagerup, O. 1952. The morphology and biology of some primitive orchid flowers. Phytomorphology. **2**.
Lindley, John. 1853. The vegetable kingdom. 3rd Ed. London.
Mansfeld, R. 1954. Über die Verteilung der Merkmale innerhalb der Orchidaceae-Monandrae. Flora **142**.
Pfitzer, Ernst. 1889. Orchidaceae in Engler & Prantl: Natürliche Pflanzenfamilien. **2**. Teil 6. Abt. Leipzig.
Reichenbach, H. G. 1868. Orchideae in Berthold Seemann: Flora Vitiensis. London.
Richard, L. C. 1818. De Orchideis Europaeis Annotationes. Mém. de Mus. d'Hist. Nat. **4**.
Rupp, H. M. R. 1943. The Orchids of New South Wales. Sydney.
Schlechter, Rudolf. 1928. Monographie und Iconographie der Orchideen Europas und des Mittelmeergebietes. **1**. Dahlem bei Berlin.
Vermeulen, P. 1953. The vanished stamens. Amer. Orchid. Soc. Bull. **22**.
———. 1954. Le rostellum des Ophrydées. Comptes rendus des séances du 8ième Congrès intern. de Botanique, sect. 7 et 8, p. 233.
———. 1955. The rostellum of the Ophrydeae. Amer. Orchid. Soc. Bull. **24**.
———. 1958. Orchidaceae in Flora Neerlandica **1**, afl. 5. Amsterdam.

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DATIERUNG DES BASISTORFES UNTER AMSTERDAM

B. ZWART UND J. J. FRIESWIJK
(Hugo de Vries-laboratorium – Amsterdam)

(eingegangen am 31. März 1959)

1. Einleitung

Im Rahmen der pollenanalytischen Untersuchungen, die das Hugo de Vries Laboratorium in der Umgebung von Amsterdam durchführt, sind die Torfablagerungen, die man an der Base der holozäne Ablagerungen findet, an einigen Stellen unter Amsterdam untersucht worden.

Die Untersuchungen des Basistorfes wären unmöglich gewesen ohne die freundliche Mitwirkung der Gemeinde Amsterdam, besonders der Abteilung "Grondmechanica" von "Publieke Werken". Diese Abteilung stellte uns die Bohrkerne von drei Stichbohrungen verfügbar, sowie die Daten von 36 Stich- und Ventilbohrungen. Besonders danken wir den Herren Ir. A. F. van Weele und L. Kok für ihre freundliche Mitwirkung. Prof. Dr. J. Heimans legte die erste Verbindung für diese fruchtbare Zusammenarbeit.

Wir danken den Herren Prof. Dr. J. Heimans und Prof. Dr. J. P. Bakker für ihr förderndes Interesse an unserer Arbeit.

Die Zeichnungen sind von Herrn J. Vuijk nach Entwürfen des ersten Verfassers ausgeführt, mit Ausnahme der Diagramme 5, 6 und 8.

2. Stratigraphie und allgemeiner aufbau

Die Oberfläche des pleistozänen oder diluvialen Sandes ist im Küstenstreifen von Belgien bis Dänemark mit einer dünnen Torfschicht bedeckt, die aus einer harten schwarzen und trockenen Torfmasse gebildet ist, ohne Struktur und fast ohne Reste die mit bloszem Auge zu erkennen sind (Abb. 1).

Diese Torfschicht findet man an der Basis der holozänen oder alluvialen Ablagerungen und sie wird deshalb allgemein Basistorf genannt. In holländischer Sprache ist auch der Name "Veen op grotere diepte" (Torf auf gröszerer Tiefe) im Gebrauch, während in englischer Sprache der Name "lower peat" (van Donselaar und Jonker, 1952) gebraucht wird. Der Basistorf ist im allgemeinen nur wenige Dezimeter stark, aber bisweilen erreicht er eine Stärke von einem Meter. Im letzteren Falle sind dünne Kleischichten zwischen die Torfablagerungen eingeschaltet (siehe Abb. 2).

Die Tiefelage des Basistorfes ist von der Tiefe der Oberfläche des diluvialen Sandes abhängig. Diese Oberfläche senkt sich in westlicher Richtung, so dasz die tiefste Lage im allgemeinen an der Nordmeerküste entlang gefunden wird. Nach Osten erreicht der diluviale Sand

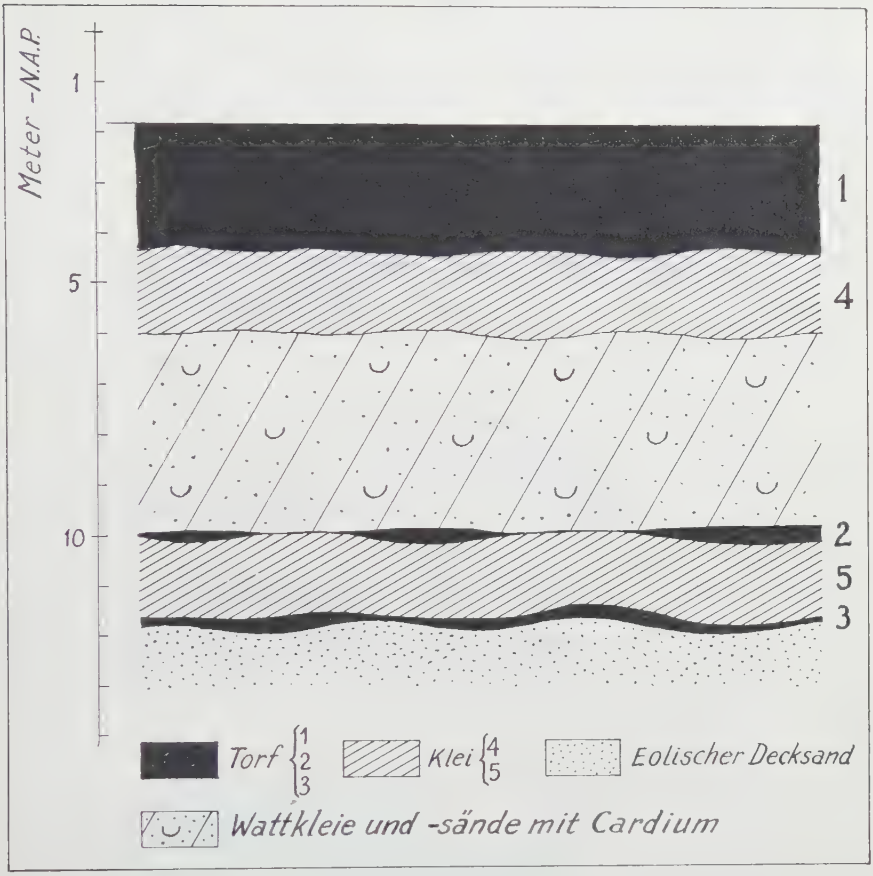

Abb. 1. Schema der alluvialen oder holozänen Ablagerungen westlich von Amsterdam.

1. Oberflächlicher Torf
2. Verspülter Torf
3. Basistorf
4. Älterer Marsch
5. Schlammklei

die Oberfläche. Die höhere Lage des Sandes hat da nur in Becken ohne Wasserabflusz Torfwuchs erlaubt.

Die Gegenden, wo der diluviale Sand nicht bis an die Oberfläche reicht, besitzen nur eine sehr schmale Zone ununterbrochener Torfablagerung. Die Entwicklung des Torfwuchses fing 10.000 bis 7000 Jähre zurück an. Der Anfangszeitpunkt des Torfwuchses hängt mit der Höhe des Landes mit Beziehung zu der mittleren Meereshöhe zusammen. So stammt der Torf im Westen der Niederlande im allgemeinen aus der atlantischen, im Nordwesten und Norden aus der atlantischborealen oder borealen Zeit. Die Grenze zwischen borealer und atlantischer Zeit stellen wir, wie allgemein angenommen wird, auf 5500 Jahre vor Christo.

Wo die Torfablagerungen nicht eine durchgehende Ablagerung bis zur subatlantischen Zeit darstellen, sind sie durch eine dicke Schicht von Wattenkleien und Wattenstanden unterbrochen. Auf diesen atlantischen Meeresablagerungen kam es wieder zur Entwicklung einer dicken Torfschicht in der subborealen und subatlantischen Zeit.

Diese Torfschicht reicht jetzt, soweit sie nicht erodiert ist, bis an die Oberfläche. Spuren einer subborealen Transgression, von ZWILLENBERG und HENDRIKS (1954) in "Waterland", nördlich von Amsterdam, in groszem Ausmasz gefunden, wurden im untersuchten Gebiet nie gefunden. An einigen Stellen ist der Basistorf nicht vorhanden. Man findet da die Wattenablagerungen unmittelbar auf dem dilivualen Sand. Weil in den obersten Schichten des Sandes an diesen Stellen sich oft ein deutliches Bodenprofil entwickelt hat, ist es deutlich, dasz das hereindringende Meer die Torfschicht erodiert hat. (VAN DONSELAAR und JONKER 1952).

Eine dicke Schicht von grauem humosen Klei, der sogenannte Schlammklei ("modderklei") findet man unmittelbar auf dem Basistorf. Schilfhalme durchbohren diese Kleischicht. Dieser Schlammklei ist an der Grenze der Wattengebiete abgesetzt worden, wo der Torfwuchs noch Fortgang fand. Zwischen den Schlammklei und die Wattenkleie und Wattensande findet man oft eine neue Torfschicht, mit sehr wechselnder Stärke. Diese Torfschicht war an einigen Stellen nicht anwesend. Da befand sich Klei auf derselben Tiefe als Torf an anderen Stellen, der Klei war jedoch stark humos. Es sind vermutlich Reste von verspültem Torf, der beim entgültigen Einbruch des Nordmeeres in den Wattenrinnen erodiert ist. Die oberste Schicht der Wattenablagerungen wird auch von einer Kleischicht gebildet. Man nennt diese graublaue Kleischicht allgemein den "älteren Marsch" (oude blauwe zeeklei). Man findet diese Kleischicht unmittelbar unter den oberflächlichen Torf. Ein viele Meter stärkes Paket von Sanden und sandigen Kleien befindet sich zwischen die zwei genannten Kleischichte. Diese Ablagerungen enthalten viele Muscheln, wie *Cardium edule* L., *Scrobicularia plana* Da C., *Lutraria elliptica* L., *Mytilus edulis* L., *Hydrobia ulvae* Penn., *Spisula solida* L., *Mactra corallina* L., *Ensis ensis* L. und *Littorina littorea* L.

3. BODENSCHNITTE UND BOHRPROFILE

Aus den Daten dieser 36 Bohrungen sind sieben ostwest laufende Bodenschnitte zusammengestellt worden (Abb. 2). Für die Lage dieser Bodenschnitte siehe Abbildung 3 (das Quadrat E3–121). Die Stärke des Basistorfes ist im untersuchten Gebiet ziemlich gleichmäszig, meistenteils 30 bis 50 cm. Die gröszte Stärke betrug 105 cm, aber an Stellen, wo diese Stärke ganz oder doch fast erreicht wird, waren meistens Kleilinsen im Torfschicht eingeschaltet. An einer Stelle wurde kein Torf gefunden: an Bohrstelle 127. Die Basis des Torfes fällt an einigen Stellen von 50 bis 75 cm über einen Abstand von 250 m. Jedoch ist es höchstwahrscheinlich kein System von Rinnen und Rücken. Wenn derselbe Abfall schon am Anfang des Torfwuchses anwesend gewesen wäre, dann würde auch der Torfwuchs in den

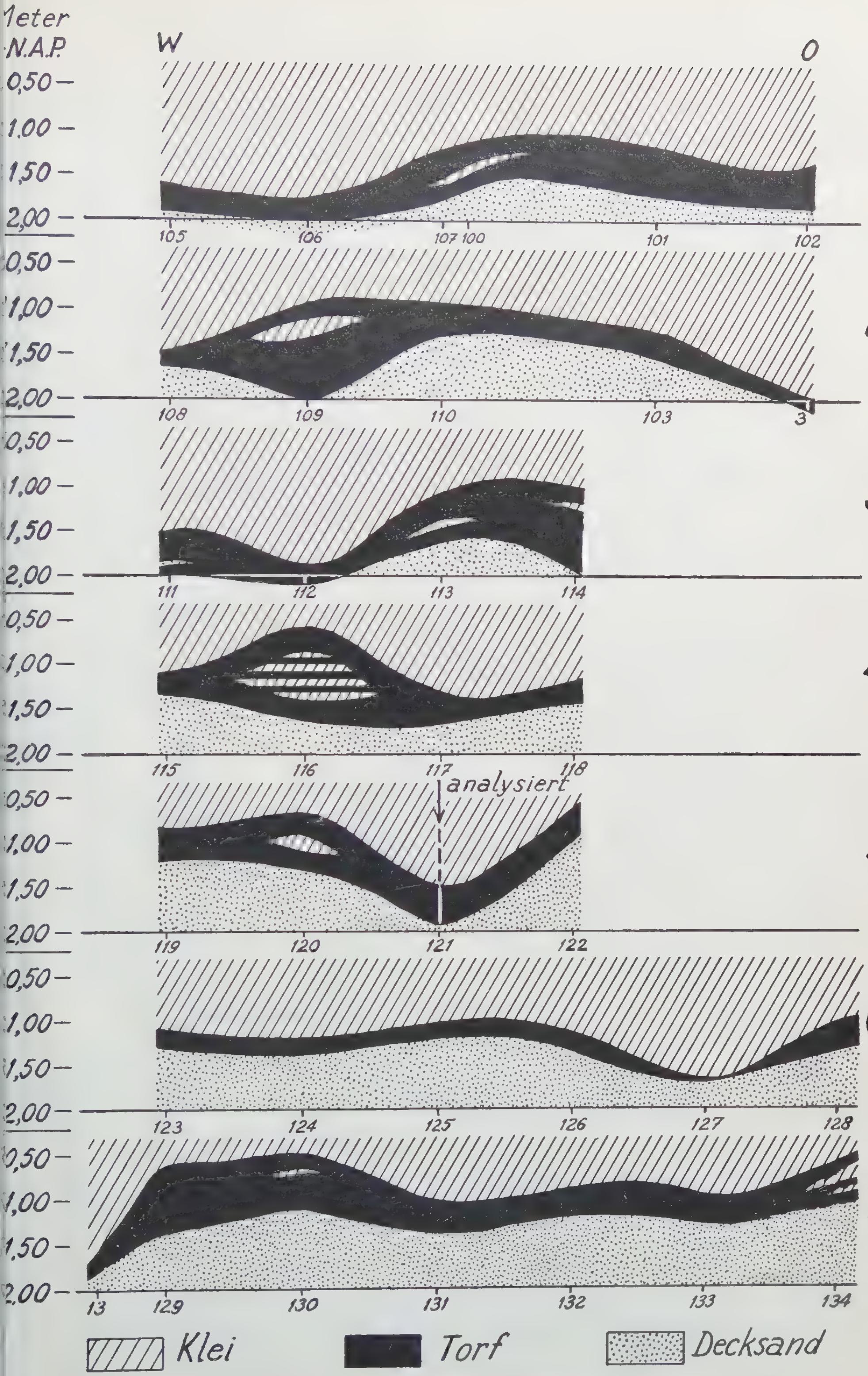

Abb. 2. Die Bodenschnitte des Quadrats bei Bohrung E3–121. Der Distanz zwischen zwei Bohrungen und Profile ist 250 m.

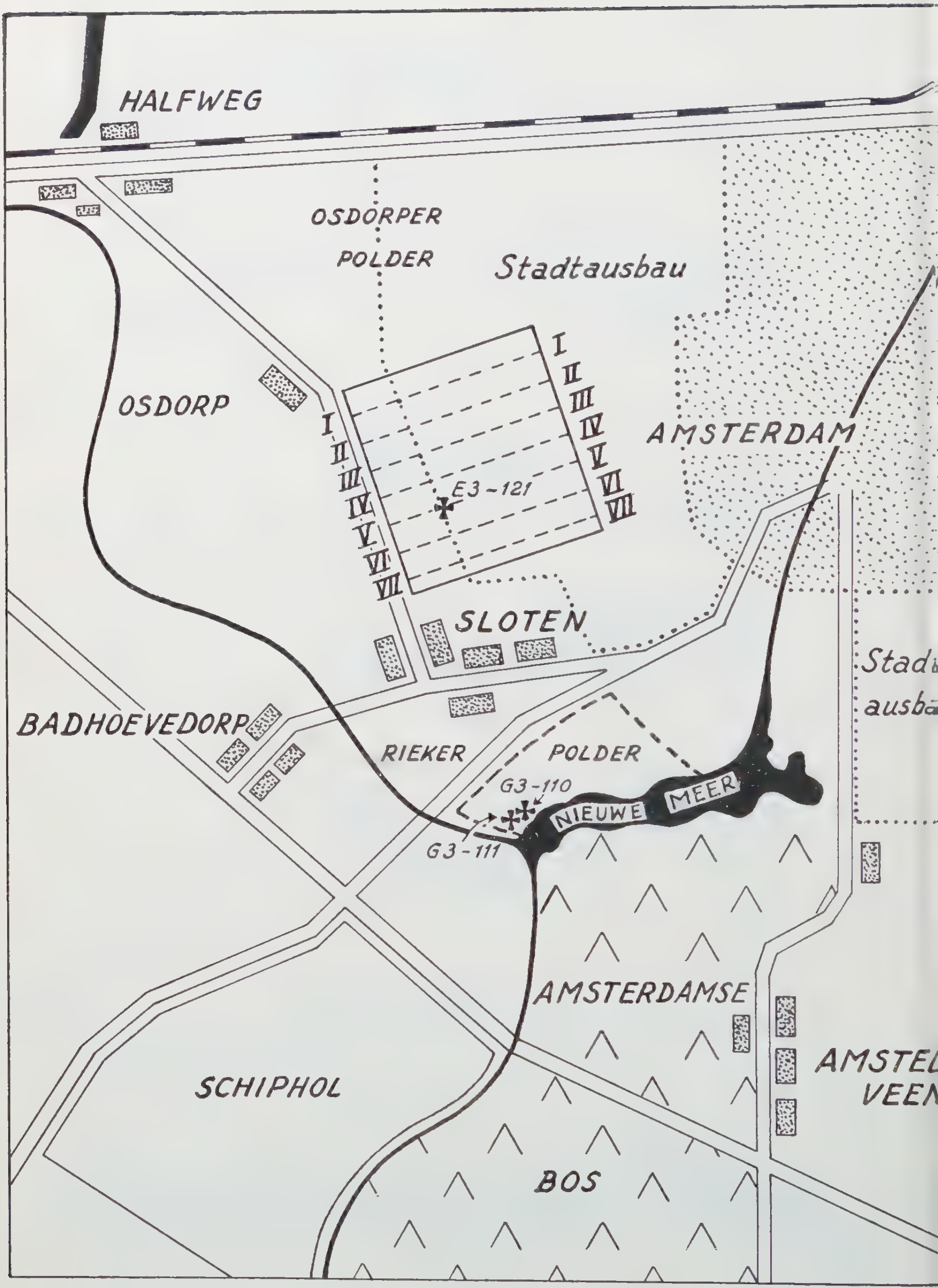

Abb. 3. Übersichtskarte des Gebietes wo die untersuchte Bohrungen verrichtet sind. Die pollenanalytisch untersuchte Bohrungen sind E3–121, G3–110 und G3–111.

Rinnen früher einen Anfang genommen haben als auf den Rücken, wie VAN DONSELAAR und JONKER (1952) in Nordwest Friesland gefunden haben. Da treten aber die Rücken und Rinnen, hier vielmehr Täler, deutlicher hervor. Sie fanden da, dasz der Torf in den Tälern nicht nur in borealer Zeit einen Anfang genommen hatte, sondern auch an einer Stelle (Tjummarum) schon in der borealen Zeit mit Meeresablagerungen bedeckt war.

Drei Argumente stehen die Hypothese, dasz die Oberfläche des Decksandes unter Amsterdam auch ein System von Rinnen und Rücken darstellen würde, im Wege:

1. Die stärkste Torfschichte sind nicht in den Rinnen abgesetzt worden. (Wir setzen voraus, dasz keine Erosion des Torfes stattgefunden hat).
2. Die Klei- und Sandlinsen, die auf flieszendes Wasser deuten, sind auch vorhanden auf den Rücken.
3. Der Torfwuchs hat auch in den Rinnen erst in atlantischer Zeit einen Anfang genommen.

Der wellige Verlauf des Torfbandes ist wahrscheinlich von der wenigeren oder gröszeren Masse der Zusammendrückbarkeit des

TABELLE I

Beschreibung der Bohrprofile

Bohrnummer E3–121		G3–110		G3–111	
Meter unter N.A.P. (mittlere Meereshöhe)	Ablagerung	Meter unter N.A.P.	Ablagerung	Meter unter N.A.P.	Ablagerung
1.90	Oberfläche	1.35	Oberfläche	1.35	Oberfläche
1.90– 4.15	schlammiger Torf	1.35– 4.35	schlammiger Torf	1.35– 4.10	schlammiger Torf
4.15– 4.90	schwerer Klei	4.35– 4.70	humoser Klei	4.10– 4.40	humoser Klei
4.90– 9.00	kleiiger Feinsand mit Muscheln (Wattensand)	4.70– 6.15	sandiger Klei	4.40–10.30	sandiger Klei
9.00–10.10	Klei mit Muscheln	6.15–10.30	Klei		
10.10–10.20	Torf				
10.20–11.50	schwerer Klei	10.30–10.88	schwerer Klei	10.30–10.58	schwerer Klei
11.50–11.87	*trockener fester Torf*	10.88–11.15	*trockener fester Torf*	10.58–10.72	*trockener fester Torf*
11.87–12.50	humoser Sand	11.15–13.55	humoser Sand	10.72–11.90	humoser Sand
12.50–	grauer Sand	13.55–	grauer Sand	11.90	grauer Sand

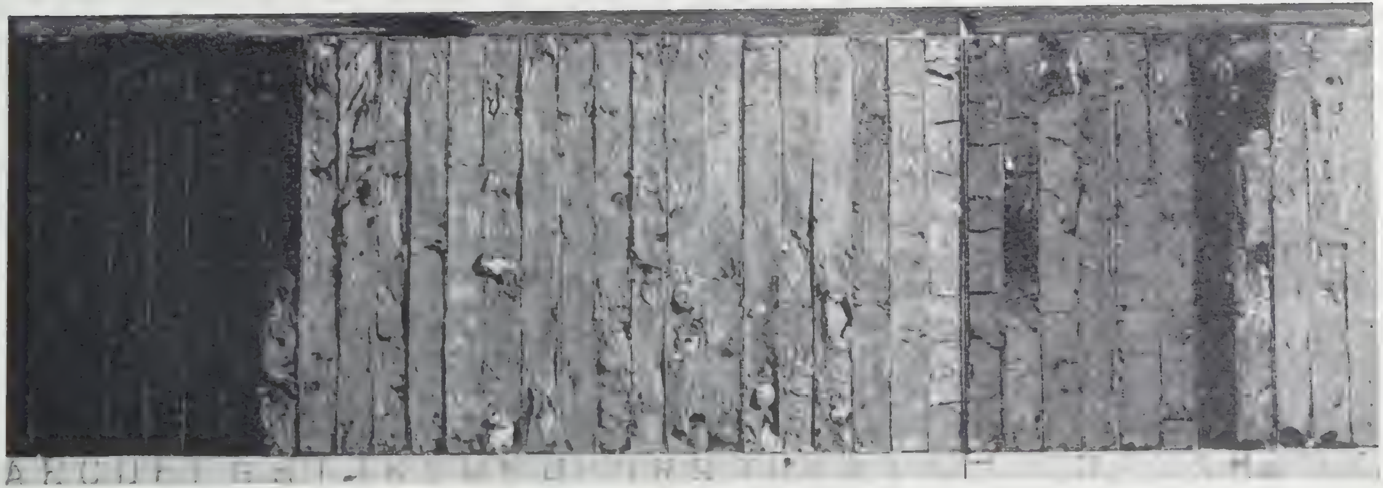

Abb. 4. Die Bohrkerne der Bohrung E3–121. Die gegenwartige Oberflache findet man links oben. Die Bohrkerne haben eine Hange von 30 cm. Jeder folgende Kern schlieszt an der Unterseite des vorgehenden an. Hintereinander findet man: 2.25 m oberflachlichen Torf (in subborealer und subatlantischer Zeit gebildet), 5.20 m Wattenkleie und Wattensande mit Muscheln, 0.10 m verspulten Torf, 1.30 m Schlammklei, 0.37 m Basistorf und darunter diluvialen Sand. Eine Erlenwurzel drangt in den Sand hinein.

(Foto Dienst Publieke Werken, Amsterdam)

Untergrundes abhängig, also von der Zusammendrückbarkeit des Tubantiens (die obersten Schichte des diluvialen Sandes).

Eine Angabe in dieser Richtung war der wechselnde Widerstand, der bei den Sondierungen in dieser Schicht gefunden wurde.

Drei Stichbohrungen sind pollenanalytisch untersucht worden, wobei der Basistorf unsere spezielle Aufmerksamkeit hatte. Für die Lage dieser Borhpunkte E–121, G3–110 und G3–111 siehe Abbildung 3. Die erste Bohrung fand statt in der Reihe von Bohrungen für die zukünftige Erweiterung der Stadt Amsterdam und die letzte zwei Bohrungen für eine Untersuchung über die Möglichkeit von Sandgewinnung.

Der Basistorf ist eine sehr zusammengedruckte harte und trockene Torfmasse mit einer schwarzen Farbe. Diese Farbe ist nicht ursprünglich. Die ursprüngliche dunkelbraune Farbe verfärbt sich schnell an der Luft zu einer schwarzen Farbe. Der Basistorf ist in den untersuchten Bohrungen nicht mehr als 36 cm stark. Halt man jedoch Rechnung mit der Zusammendrückbarkeit der ursprünglichen Torfmasse, dann könnte sie sich am Anfang der Bedeckung mit Wattenablagerungen viele Meter belaufen haben. Die Bedeckung mit Kleiablagerungen hat plötzlich stattgefunden, weil die Analyse der Oberfläche des Torfes keine Übereinstimmung hat mit der Analyse der untersten Kleischicht. Zudem ist die Grenze Torf-Klei ziemlich scharf zu nennen. (siehe auch Abb. 4).

4. Die ergebnisse der pollenanalytischen untersuchungen

Von jedem drei Zentimeter des Basistorfes der Bohrungen E3–121, G3–110 und G3–111 ist ein Muster genommen. Wir nahmen den Musterabstand kurz, Rechnung haltend mit der Zusammenpressung der Torfschicht. In den Pollendiagrammen sind die Prozentsätze der Kräuter, Moose und Farne bezogen auf die Baumpollensumme, in der *Corylus* oder *Myrica nicht* einbegriffen ist. Die Prozentsätze dieser letzteren Pflanzen sind auch auf die Baumpollensumme bezogen.

In den Diagrammen der Bohrung G3–110 und G3–111 (Abb. 5 und 6) findet man die bekannte *Pinus-Alnus*-Kreuzung, wo die Grenze zwischen die boreale und atlantische Zeit gelegt wird, ganz unten in der Torfsäule. Diese Kreuzung fehlt im Diagramm von Bohrung E3–121 (Abb. 7). Wenn wir nicht annehmen, dasz die Pollenkörner aus dem Torf ins Sand herunter gespült sind, können wir sagen, dasz an einigen Stellen der diluviale Sand nicht im Diluvium abgelagert worden ist. Pollenkörner können selbstverständlich durch Einspülung den Sand herein gedrungen sein. Es ist doch unbegreiflich, dasz die von Ursprung eolischer Sandablagerung keine Zunahme an *Pinus*pollen zu sehen gibt. Der Basistorf hat sich also unter Amsterdam ganz oder doch fast in atlantischer Zeit entwickelt.

Die Tiefelagerung des Torfes hat jetzt keine Korrelation mehr mit dem Anfang seines Wuchses, denn im Provinz Nord-Holland befindet der Torf sich auf viel gröszerer Tiefe als in Friesland, obgleich es im letzteren Gebiet eine etwas ältere Ablagerung bildet.

Die Oberfläche des diluvialen Sandes hatte an der Grenze zwischen

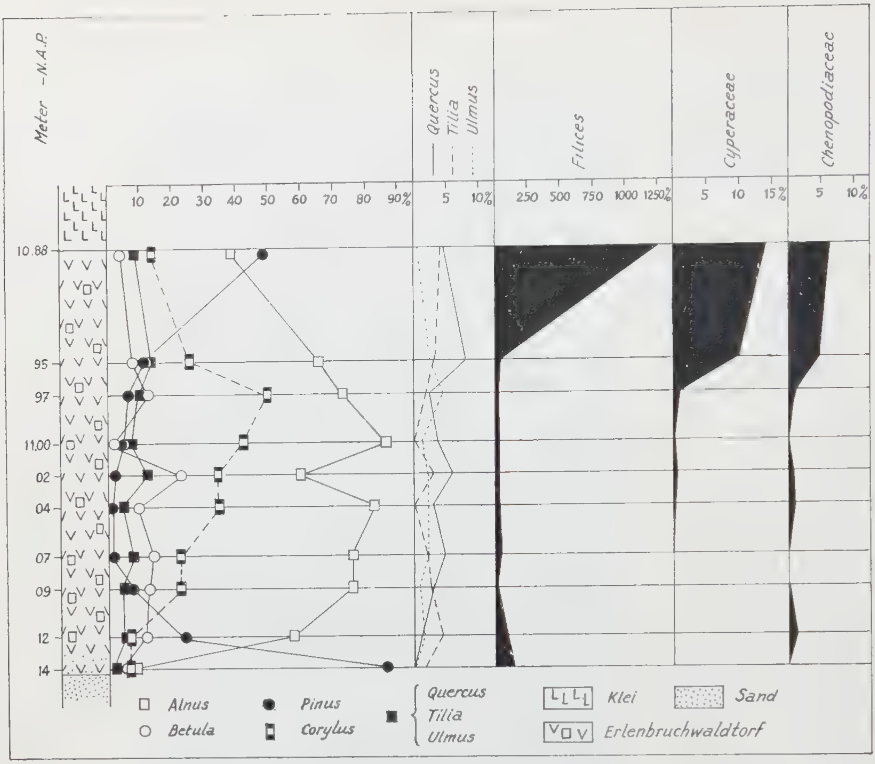

Abb. 5. Pollendiagramm des Basistorfes von Bohrung G3–110.

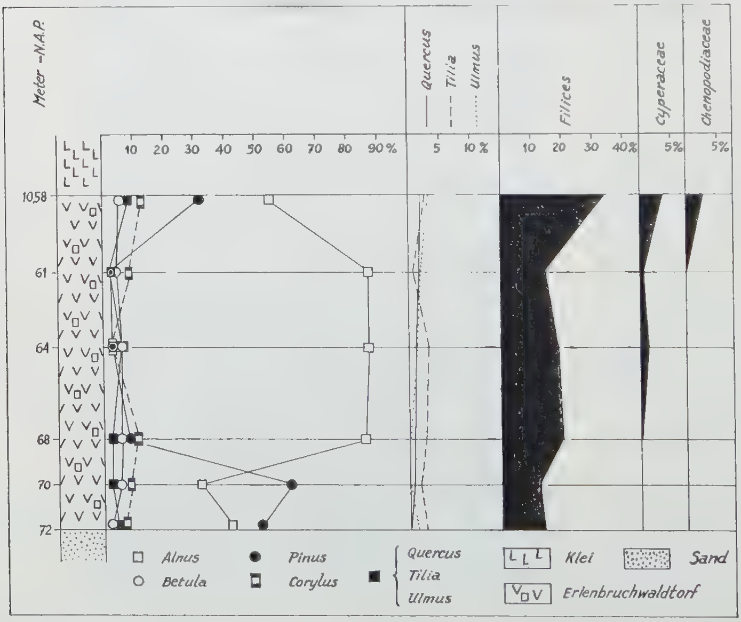

Abb. 6. Pollendiagramm des Basistorfes von Bohrung G3-111.

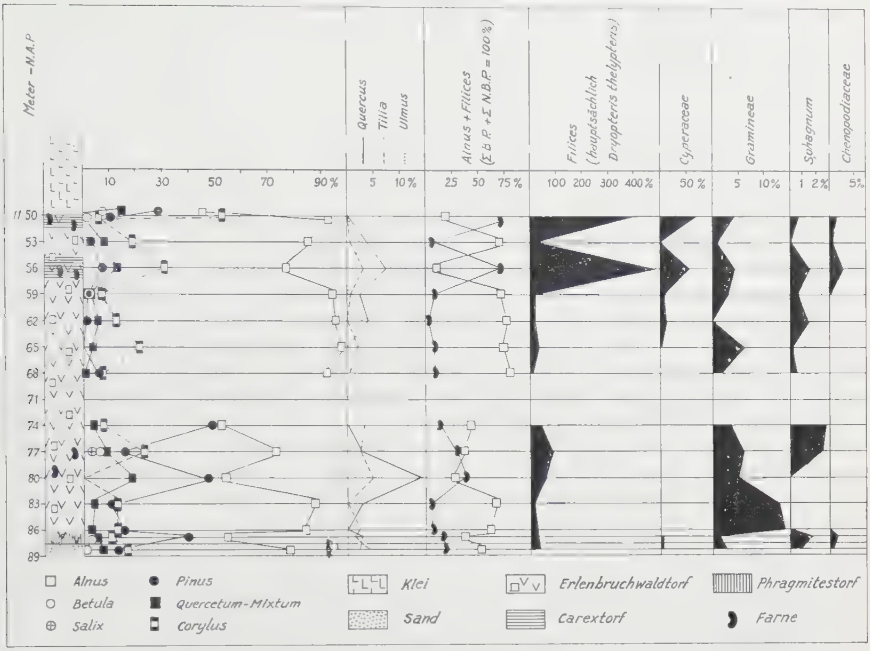

Abb. 7. Pollendiagramm des Basistorfes von Bohrung E3–121.

borealer und atlantischer Zeit vielleicht ein anderes Profil als heute in der Tiefe gefunden wird.

5. DIE ZUSAMMENSETZUNG DES BASISTORFES

Der Torf war ganz aus Resten von *Alnus* und *Dryopteris thelypteris* Gray gebildet. Die letztere Pflanze ist eine Charakterart für das Alnetum in West-Europa. Die Abwechslung in der Farnespuren und Pöllenkörner von *Alnus* ist auffallend, besonders wenn man diese Zahlen als Funktion der totalen Zahl an Pollenkörner aussetzt (Methode Iversen). Diese Abwechslung könnte zeigen auf eine Änderung der Landschaft sowohl im Raum, wie in der Zeit: eine Abwechslung von Erlenbruchwälder mit Farnemooren. Nicht nur die Anwesendheit vieler mikroskopischen Resten von *Alnus* und *Dryopteris* sprichen für diese Zusammensetzung der alten Landschaft, sondern auch die absolute Pollenarmut anderer Arten. Das Ausschlieszen des Alnuspollens hat wenig Bedeutung, weil auch die Umgegenden vermutlich dieselbe Landschaft gezeigt hatten. (Janssen, 1959).

Der wie *Corylus* gezählte Pollen ist sehr wahrscheinlich *Myrica*pollen. Die letztere Pflanze kommt viel in einem Alnetum mit sauerem Untergrund vor. Die stark erodierten Pollenkörner waren nicht mit voller Sicherheit zu trennen vom *Corylus*pollen.

6. KORRELATION MIT UMGEBENDER GEBIETE

Der Basistorf der südlichen Tunnelgrube bei Velzen ist von FLORSCHÜTZ (1944) analysiert worden (Abb. 8). Die untere Hälfte war in der borealen Zeit und die obere Hälfte in der atlantischen Zeit gebildet. Die entgültige *Pinus-Alnus*-Kreuzung befindet sich in der Mitte der Ablagerung. Die Lage des Torfes ist hier 16.55 bis 16.77 m unter die mittleren Meereshöhe, während bei Amsterdam die Tiefelage wechselt von ungefähr 10 bis 12 m unter die mittlere Meereshöhe. Der Basistorf war bei Velzen nicht eine reine Torfablagerung, nur die Base und dir oberste Schicht sind aus Torf gebildet. Zwischen diese Torfschichte fand man Klei. Florschütz hat in diesem Klei Reste einer Meerestierwelt und einer Brackwassertierwelt gefunden. Die Bildung des Torfes unter Velzen sollte schon vom Anfang den Einflusz des Meeres erfahren haben. Jede Spur dieses Meereseinfluszes fehlt bei der Torfbildung unter Amsterdam. Nur am Ende der Torfbildung zeigt ein Hervortreten der *Chenopodiaceae* und *Cyperaceae* auf einer allmähligen Ver-

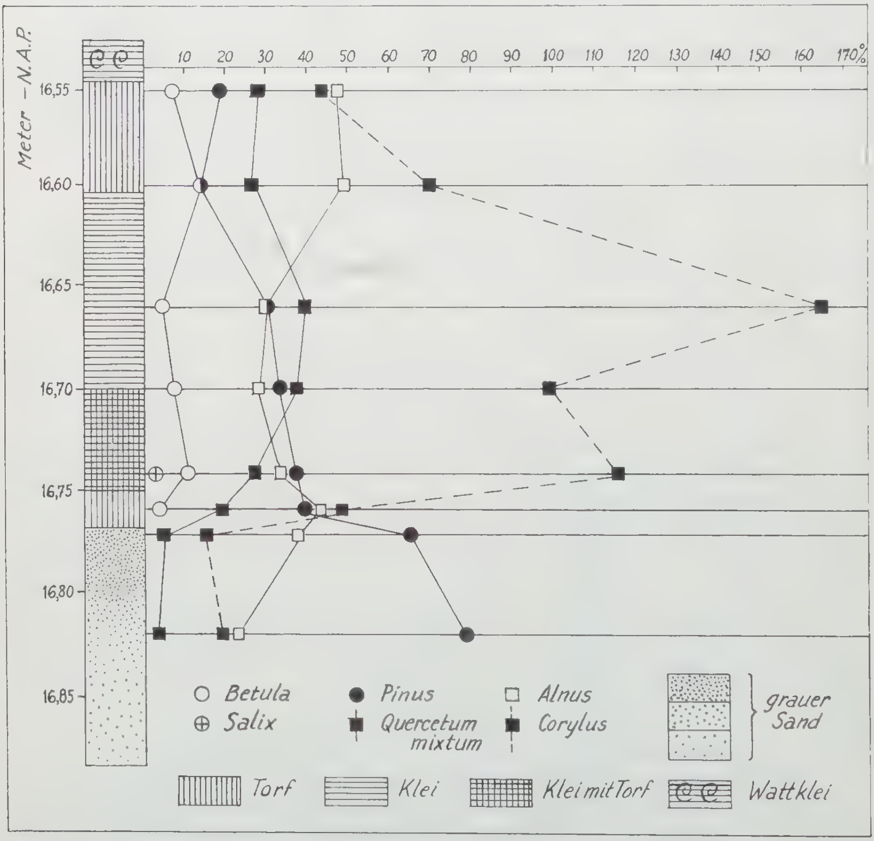

Abb. 8. Pollendiagramm des Basistorfes aus der Tunnelgrube bei Velzen. (Nach Florschütz, 1944).

salzung des Grundwassers. Das Grundwasser ist schlieszlich bis oben die Landoberfläche emporgestiegen und dann kam es zur Ablagerung des Schlammkleies.

Die Entwicklung des Basistorfes unter Amsterdam hat erst einen Anfang genommen als unter Velzen schon ein Paket Torf und humoser Klei abgelagert worden war.

Die gegenwärtige Differenz in der Tiefelage des Basistorfes unter Amsterdam und Velzen (6 Meter) möchte eine Erklärung sein für das verschiedene Alter des Torfes, obgleich wir nicht wissen, ob diese Niveaudifferenz schon am Anfang der atlantischen Zeit anwesend war. Die gegenwärtige Oberfläche des diluvialen Sandes reicht im Süden der Provinz Nord-Holland bis 11 m unter die Bodenoberfläche. In der Mitte der Provinz Nord-Holland senkt sie sich 20 m oder mehr unter die Bodenoberfläche um nördlich von diesen Gegenden wieder emporzureisen. Man findet hier ein deutliches System von Horsten und Slenken.

Beim Vergleichen des Alters des Basistorfes unter der Provinz Nord-Holland mit dem unter der Provinz Friesland ist diese Erklärung nie verwendbar.

Die Oberfläche des diluvialen Sandes unter der Provinz Friesland möchte ursprünglich eine andere Lage als heute gehabt haben in Hinsicht auf der Lage der Oberfläche des Sandes unter Amsterdam. Es ist selbstverständlich dasz der Untergrund unter Amsterdam einem gröszeren Sinken unterlegen ist als der unter Friesland. Ursprünglich könnte die Tiefelage dieser zwei Oberflächen gerade entgegengesetzt gewesen sein. Es wäre ebenfalls möglich, dasz das Meer bei Friesland durch eine durchbrochene Nehrung früher Zutritt zum Hinterland hätte.

ZUSAMMENFASSUNG

Der Basistorf (Torf an der Basis der holozänen oder alluvialen Ablagerungen) unter Amsterdam ist nach der Analysen von drei nach einander 27, 14 en 36 cm langen Torfsäulen ganz oder fast ganz in der atlantischen Zeit gebildet. Analysen des Torfes an anderen Stellen unter Amsterdam (noch nicht publiziert worden) bestätigten diese Ergebnisse.

Wenn wir die gegenwärtige Tiefelage des Basistorfes berücksichtigen, dann stimmt das Alter des Torfes mit dem Alter des Torfes unter Velzen gut überein. Man findet aber keine Übereinstimmung mit der gegenwärtigen Tiefelage des Basistorfes unter dir Provinz Friesland, aber diese Differenz in Tiefelage ist wahrscheinlich die Folge späterer tektonischen Bewegungen.

Der Basistorf unter Amsterdam war über seine ganze Länge namentlich aus Resten von *Alnus* und *Dryopteris thelypteris* Gray. gebildet, wobei im unteren Teil die Erlen und im oberen Teil abwechselnd Erlen und Farne die Oberhand gewonnen. Der obere Teil des Torfes war auch teilweise gebildet von Schilfen und Seggen. Auffallend war die Armut an Arten des analysierten Pollens.

LITERATUR

Andel, Tj. van. 1949. Geologie en Mijnbouw **11**: 171.
Donselaar, J. van und Jonker, F. P. 1952. Acta Bot. Neerl. **1**: 259.
Faber, F. J. 1947. Geologie van Nederland, deel **3**. Gorinchem.

FLORSCHÜTZ, F. 1934. Tijdschr. Kon. Ned. Aardr. Gen. **51**: 1.

——— und I. M. VAN DER VLERK. 1939. De Maastunnel **2**: 1.

— ———. 1944. Tijdschr. Kon. Ned. Aard. Gen. **61**: 25.

JANSSEN, C. R. 1959. Acta Bot. Neerl. 8: 55.

PANNEKOEK, A. J. u.a. 1956. Geologische geschiedenis van Nederland. 's Gravenhage.

VERMEER-LOUMAN, G. G. 1934. Pollen-Analytisch onderzoek van den West-Nederlandschen Bodem. Dissertation. Amsterdam.

VROMAN, M. 1952. Acta Bot. Neerl. **1**: 250.

WIGGERS, A. J. 1955. De wording van het Noordoostpoldergebied. Dissertation. Zwolle.

ZWART, H. J. 1951. Proc. Kon. Ak. Wet., Ser. B: 162.

ZWILLENBERG, L. O. und J. HENDRIKS. 1954. Geologie en Mijnbouw **16**: 105.

BRIEF REPORTS

MANTEN, A. A.: Pollen-grain size and its value in Palynology

In prequaternary palynology identification of the pollen-grains with natural genera and species often proves to be impossible or very difficult. Therefore organ genera and species had to be created. The organ species, however, are not rarely large and sometimes ill-defined, viz. when they show transitions from one to another. Moreover, for stratigraphical use a subdivision may be desirable. Then, in the absence of good diagnostic characters of a qualitative nature often the dimensions of the pollen grains are called to aid. Examples are not difficult to find. Here some will be mentioned taken from the pollen atlas of THOMSON and PFLUG (1953):

Pityosporites microalatus (R. Pot) Pf. et Th. — the *Pinus haploxylon* type — is divided into two forms: *major* (70–110 μ) and *minor* (45–70 μ).

Tricolporopollenites kruschi (R. Pot.) Pf. et Th. (Nyssa?) is divided into five subspecies, three of which differ according to the diagnosis only in their dimensions.

The *Ilex*-like pollen grains are classified in two organ species: *Tricolporopollenites iliacus* (R. Pot.) Pf. et Th. and *Tricolporopollenites microiliacus* Pf. et Th. For the latter diagnostic characteristics are given that are found in *Tricolporopollenites iliacus* too. Only the dimensions are different (*T. microiliacus* 15–25 μ; *T. iliacus* 25–50 μ). *T. iliacus* is subdivided into two forms: *major* (more than 45 μ) and *medius* (25–45 μ).

The organ species *Triatriopollenites coryphaeus* (R. Pot.) Pf. et Th., from the group *Myricaceae/Betulaceae*, is subdivided into two subspecies: *punctatus* (R. Pot.) Pf. et Th. and *microcoryphaeus* (R. Pot.) Pf. et Th. Pollen grains from the subspecies *Triatr. coryph. microcoryphaeus* are often identified with Engelhardtioid pollenforms. There are, however, all possible transitions to the *Myricaceae* and *Betulaceae*. Therefore, a border line is taken at 18 μ. All pollen grains of this type that are smaller than this measure are referred to the subspecies *microcoryphaeus*. When THOMSON in his diagram of the quarry "Fortuna" represents the percentage of Engelhardtioid pollen-forms, he only means the percentage *Triatr. coryphaeus microcoryphaeus*. In this diagram (THOMSON 1950) can be seen that there is some relation between the curves for Engelhardtioid pollen-forms and that for *Myricaceae/Betulaceae*. This also is likely, for, when in this case all dimensions are present, it is a strange supposition that *Engelhardtia* should only have provided pollen-grains up to 17,9 μ and the *Myricaceae* and *Betulaceae* only of 18.1 μ and larger. TRAVERSE (1955, p. 45) even mentions as size of *Engelhardtia* pollen-grains an average of ca. 28 μ, with maximum dimensions up to 32 μ.

It has been found that the so-called Engelhardtioid pollen-forms are most numerous in the older tertiary, in younger deposits their percentage decreases. Even in the diagram of the Rhenish browncoal formation can be seen that these smaller pollen types are more common at the bottom than at the top. It is not quite clear, however, what botanical conclusion may be drawn from this.

TABLE I

The rank correlation test of KENDALL applied to data from a palynological study of the miocene browncoal in the quarry "Anna" (SE. Netherlands).

Column I: Percentages of pollen grains from the bog vegetation *(Myricaceae/ Betulaceae + Cyrillaceae + Ericales)* in 32 samples.
Column II: Percentages of pollen grains from the vegetation round the bog *(Pinaceae + Salicaceae/Platanaceae + Fagaceae)*.
Column III: Quotient bog vegetation/surrounding vegetation.
Column IV: Percentages of *Triatriopollenites coryphaeus micro-coryphaeus.*

I	II	III	IV
38,0	37,2	1,02	2,8
39,2	40,0	0,98	2,8
40,0	46,4	0,86	0,4
42,0	38,8	1,082	4,4
40,4	43,6	0,93	2,4
46,4	34,4	1,35	2,4
43,2	40,0	1,080	3,2
47,2	36,8	1,28	2,0
38,0	40,4	0,94	2,0
42,0	41,6	1,01	3,6
34,4	36,4	0,95	5,6
44,0	46,0	0,96	2,4
38,8	43,2	0,90	3,2
33,6	39,6	0,85	6,0
44,8	30,8	1,45	6,0
42,4	31,6	1,34	4,8
40,4	30,4	1,33	9,2
54,4	21,2	2,57	12,4
47,6	29,2	1,63	4,0
38,8	42,8	0,91	0,8
36,8	42,4	0,87	1,6
35,6	46,8	0,76	4,4
36,4	50,0	0,73	4,4
48,4	32,4	1,49	2,8
30,4	55,2	0,55	4,0
33,2	46,0	0,72	2,0
69,2	19,6	3,53	4,0
60,4	28,0	2,16	4,0
39,2	33,2	1,18	4,0
40,4	43,2	0,94	6,8
37,2	36,0	1,03	8,0
36,4	28,0	1,30	5,6

Engelhardtia is a tall tree and, as TRAVERSE (1955, p. 25) in his study of the Brandon lignite of Vermont (U.S.A.) rightly remarks, "presumably grew near, not in the swamps of the basin of deposition." Thus, when *Triatriopoll. coryphaeus microcoryphaeus* may be identified with *Engelhardtia* pollen, a definite connection may be expected in a pollen diagram, between the percentages found for the *microcoryphaeus* pollen-grains and those of the pollen-grains from the vegetation surrounding the bog. As an example data were taken from a palynological study of the browncoal in the quarry "Anna", Dutch Limburg (MANTEN, 1958), see table. The author checked whether there exists a correlation between the quotient of the percentages of pollen-grains from the bog vegetation and those of the pollen-grains from the surrounding vegetation (magnitude A, table, column III) and the frequencies of *microcoryphaeus* pollen-grains (magnitude B, table, column IV). For this it has been examined whether at increasing A, magnitude B also increases (positive correlation), or just decreases (negative correlation), or shows no distinct course (no correlation). According as the correlation is positive or negative it may be concluded that the *microcoryphaeus* pollen-grains have come mainly from the bog vegetation, respectively from the forests round the bog.

Correlation was tested by means of Kendall's rank correlation test (KENDALL 1948). For this the figures from column III were arranged in an ascending series; the percentages from column IV, belonging each to a special figure from column III, were rearranged accordingly. Each of these samples then was compared with every other sample, and for each pair a value +1, —1 or 0 was scored according as the two samples agreed or disagreed in their rankings or were tied. The 32 samples yielded 496 comparisons with 293 scores +1, 178 scores —1 and 25 scores 0, resulting in a value +115 for KENDALL's statistic S. The significance of the deviation of this value from the value 0, expected under the hypothesis that no correlation exists, can be judged by the probability $P] \mid S \mid \leqslant 115]$, which is found to be 0,062 if the distribution of S is approximated by a normal distribution with the same mean and variance. This probability is sufficiently low to justify the conclusion that there exists a positive correlation between the two characteristics.

This implies that the greater part of the pollen-grains in the subspecies *Triatriopoll. coryphaeus microcoryphaeus* must have come from plants living in the browncoal. Because *Engelhardtia*, as mentioned above, is a tall tree, not growing in the bog, this is a very strong indication that the *microcoryphaeus* pollen-grains have not originated from *Engelhardtia*. Presumably they came from *Myricaceae/Betulaceae*, as is the case with the other *Triatriopollenites* forms. The border line of 18 μ without other characteristics thus *does not have any diagnostic value.*

SUMMARY

A subdivision of pollen types based only on different dimensions is very dubious. An example is given, taken from the miocene browncoal in the Lower-Rhine area of Germany and the Netherlands.

REFERENCES

KENDALL, M. G. 1948. Rank correlation methods, Griffin & Co. London.

MANTEN, A. A. 1958. Palynology of the miocene browncoal mined at Haanrade (Limburg, Netherlands). Acta Botanica Neerlandica **7**: 445–488.

THOMSON, P. W. 1950. Grundsätzliches zur tertiären Pollen- und Sporenmikrostratigraphie auf Grund einer Untersuchung des Hauptflözes der rheinischen Braunkohle in Liblar, Neurath, Fortuna und Brühl. Geol. Jahrb. **65**: 113–126.

——— und H. PFLUG. 1953. "Pollen und Sporen des mitteleuropäischen Tertiärs". Palaeontographica, **94**, Abt. B.

TRAVERSE, A. 1955. Pollen analysis of the Brandon lignite of Vermont. Bureau of Mines Report of Investigations **5151**.

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BOOK REVIEWS

OF PUBLICATIONS RELATED TO BOTANICAL WORK IN THE NETHERLANDS

BOGAERS, J. E., W. GLASBERGEN, P. GLAZEMA and H. T. WATERBOLK (ed.): Honderd Eeuwen Nederland (The Netherlands in the past Hundred Centuries). Special issue of Antiquity and Survival, vol. 2, no. 5–6, 314 pp., The Hague, 1959, "Luctor et Emergo", Mercuriusweg 37. Dfl. 17.30 (paper) or 19.80 (cloth).

In this new, copiously illustrated book a large number of authors deal with various topics as archeology, prehistory, folklore, etc. of the Netherlands. Two botanists, Dr. H. T. WATERBOLK and Dr. W. VAN ZEIST have written the first two chapters. Professor WATERBOLK in the first chapter (p. 12–26) deals with the dating and age measurements by means of the radiocarbon method as practised in the department of physics of Groningen University. The second chapter by Dr. VAN ZEIST (p. 27–36) is entitled "Botanical Investigations and Prehistory". It deals with the results of pollen analysis as far as it is important to the investigation of the activities of early human cultures.

The book is in Dutch but subtitles of the illustrations in some chapters are also in English.

F. P. J.

Acta Botanica Neerlandica **8** (1959) 373–421*)

INVESTIGATIONS INTO THE CHEMOTHERAPEUTIC ACTIVITY OF NITROSO HYDROXYARYL COMPOUNDS TOWARDS SOME VIRUS DISEASES

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*) Also published as a separate thesis with page numbers 363–411.

I. INTRODUCTION

The economic importance of virus diseases in plants is often very considerable on account of the serious losses these diseases may cause. This refers to plants which are perennial or are propagated vegetatively, but also to annual and biennial crops raised from seed when they are infected in an early stage. Viruses disturb the normal metabolic processes in the whole plant and once they have penetrated they persist indefinitely in its vegetative parts, as there is no recovery from most virus diseases. Moreover, the losses thus incurred are increased by the viruses spreading very rapidly through insect vectors.

A most effective way of avoiding virus diseases would be growing virus-resistant varieties, but only a few cases of real immunity are known. Another possibility is growing varieties with a high degree of virus tolerance, so that the yield of the crop is not much affected by the infection. The results obtained with this method have been more encouraging. The use of virus-free plant material and variation of normal cultural practice can give better results, but only if sufficient precautions are taken to isolate the plants from the sources of infection. By far the most effective way is to destroy the virus-diseased plants and to kill the insect vector with insecticides. Much work has been done in this field with good results.

Nevertheless, none of these methods has led to complete elimination of the virus diseases. Attempts have therefore been made to destroy the virus in the cells of the host plant without impairing the viability of these cells. In this respect various physical treatments, e.g. ultraviolet, infra-red or X-ray radiation, or heat treatment might offer possibilities. Heat therapy against viruses with a low thermal inactivation point has in some cases been successful, although this method is unlikely to be generally applicable. A curing effect of the radiation of infected plants has not been reported.

Such methods, however, involve the risk of experimental error. Under the influence of the treatment symptoms may be masked, when the virus remaining unaffected. Thus, Thung (1949) found that, tobacco mosaic virus was inoculated, at certain elevated temperatures the symptoms were completely masked, but the virus remained active and the symptoms appeared as soon as the plants were kept at lower temperatures.

Stoddard (1942) was one of the first to point to the possibility of chemotherapeutic treatment of plants. He had found that bud wood from peach trees infected with X disease can be cured by soaking it in solutions of quinhydrone, urea or sodium thiosulphate, but this experiment still needs confirmation. Although the chance of finding substances that are indeed chemotherapeutically active may be considered rather small, it seemed worth while to investigate various compounds in this respect.

Chemicals can have a preventive or a curative effect. A compound is preventive when it prevents the virus from penetrating into the plant or from spreading if it does penetrate. Only when a compound attacks the virus itself and inhibits its synthesis, which results in the plant being cured, it has a curative effect. A disadvantage of curative chemotherapeutics is that the disturbing influence of the virus may remain visible at the end of the treatment, particularly in the full-grown parts of the plants, since symptoms as necrosis, leaf roll or mosaic patterns cannot be expected to disappear altogether.

Compounds with preventive activity are the most attractive, as the plant remains healthy. From the results obtained by other investigators and of personal experience it does not seem likely that such compounds have already been found; mostly, the virus multiplication is retarded, which makes the consequences of an infection less serious.

When a chemical proves to have chemotherapeutic activity, it is often difficult to demonstrate which of the two effects plays a role.

BAWDEN (1954) distinguishes between inhibitors of infection and inhibitors of virus increase. The former prevent infection when inoculated into leaves simultaneously with virus; the latter retard the multiplication rate of the virus in the plant when applied to leaves already infected.

This distinction is similar to that between substances with a preventive and with a curative effect. Table I lists a number of compounds, natural or synthetic, that are inhibitors of infection.

Some, if not all, of these compounds may have inactivated the virus in vitro already, before it reaches the plant, as a result of interaction between virus and chemical. They may also act at the time

TABLE I

Some inhibitors of infection mentioned in the literature

Compounds	Virus	Host plant	Authors
Natural compounds			
trichotecine roseum	TMV	tobacco French bean	BAWDEN and FREEMAN (1952) BAWDEN (1954)
leaf extracts containing tannin, tannic acid, geraniatannic acid, extracted from strawberry, raspberry and other leaves	TMV tobacco necrosis virus rattle virus	tobacco	HIRTH (1953) TRESH (1956) THUNG and VAN DER WANT (1951) PFANKUCH (1943)
enzymes, sera, extracts from bacteria fungi higher plants insects (65 substances mentioned)	TMV	tobacco	BARTELS (1955 *a*, *b*, 1956)
extracts from carnations	TMV	tobacco	NOORDAM, THUNG and VAN DER WANT (1951) VAN DER WANT (1951) RAGETLI (1957)

TABLE I (continued)

Compounds	Virus	Host plant	Authors
B. *Synthetic compounds*			
thiouracil	TMV	tobacco	BAWDEN (1954)
trisodium phosphate	potato virus X TMV	potato tobacco	BROCK (1952)
cyanide hydroxylamine iodoacetate	TMV	tobacco	CHIBA and Coworkers (1954
formaldehyde	TMV	tobacco	CARTWRIGHT and LAUFFER (1954) HIRAYAMA (1954) KNIGHT (1951)
sodium chloride potassium chloride	potato virus X	potato	KANNGIESSER and DEUBNER (1954)
iodine phenyl isocyanate carbobenzoxy chloride (benzochloro formate) p-chlorobenzoyl chloride benzenesulphonyl chloride	TMV	tobacco	KNIGHT (1951)
victoria blue Browning No. 47 and other dyes tannins serum globuline octyl-X decyl-X dodecyl-X, etc. X = dimethylbenzyl ammonium chloride	TMV	tobacco	PFANKUCH (1943)
lysine polypeptides	TMV	tobacco	BURGER and STAHMANN (1951
several chemicals, including: dyes proteins and protein derivatives amino acids nucleic acid derivatives plant growth substances polypeptides enzymes	TMV	tobacco	DALE and THORNBERRY (1955)

the virus just comes into contact with the plant, by taking the receptor place and thus preventing infection (THUNG 1952, RAGETLI 1957).

The investigations described in this publication were set up with the aim of finding compounds having an “in vitro” antivirus activity, i.e. in the plant. Greenhouse experiments with young plants were done to establish what compounds displayed chemotherapeutic activity without being phytotoxic. The best of these were further tested in the field, where the plants could be examined till their mature stage. The results of both the greenhouse and the field tests are discussed in the last chapter in the light of additional data on "in vitro" effect, serology and chemical properties.

As the virus synthesis (which has not been investigated) is of a different pattern in various plants, it was desirable to include in this investigation as many different viruses and plants as possible in order to obtain the greatest possible validity of results. For practical reasons, however, this number had to be reduced considerably. Still, to make the spectrum as wide as possible, four different types of virus, viz. tobacco mosaic virus, yellow virus and two bean viruses, and seven types of plants belonging to different families of the Dicotyledones were used. With this selection diseases having their strongest influence on either leaf-, root- or seed production were generated.

The choice of these viruses and plants was determined by their economic importance in Western Europe.

The losses caused by tobacco mosaic virus (TMV) are very considerable. For tobacco Bawden (1950) estimates them at as much as 4.10^6 pounds per year in the USA alone; in England, the yield of greenhouse tomatoes is reduced by at least 10 % every year. The total loss caused by TMV cannot be given because this virus is spread throughout the world.

Virus yellows in sugar beet is spread over the whole Western and Southern part of Europe and is even reported to occur in Turkey, Syria and Persia (Schlösser, 1952); it has also been found in the USA (Coons, 1952) and recently in the USSR (Goryuskin and Kokhan, 1958). The damage caused by this disease varies every year. In the Netherlands and Belgium the losses vary from 10–40 % of the total sugar production; in one area the damage is often much more serious than in another. According to Hull (1953) diseased plants produce weekly 4.5 % less sugar than healthy ones. In years of heavy attack the weight of the root crop drops considerably and losses of 40–60 % may be found; it is remarkable that mostly the sugar content does not decrease by more than 1 %.

The bean viruses cause losses every year. For the Netherlands exact data are not available; in the USA the annual losses due to bean mosaic diseases are estimated at several million dollars (Zaumeyer and Rex Thomas, 1953).

II. MATERIAL AND METHODS

1. Plant material

For the investigation the following plants were selected:

a. Tobacco
   1. *Nicotiana tabacum L.* var. White Burley or var. no. 11
   2. *Nicotiana rustica L.*
   3. *Nicotiana glutinosa L.*

The seeds had been obtained from our own plants and showed great uniformity in germination.

b. Sugar beet, *Beta vulgaris L.* var. Kuhn P.[1]
This variety has been grown from crossings of different families in order to adapt it to geographical and climatological circumstances, so that the seedlings always grow under optimum conditions.

c. Beans
   1. French bean, *Phaseolus vulgaris L.* var. Beka [2]
   2. Broad bean, *Vicia faba L.* var. Driemaal wit [3]

d. Tomato, *Solanum lycopersicum L.* var. Ailsy Craig [3]

2. Cultivation of plants

The plants were cultivated in the greenhouse in a soil mixture containing leaf mould, farmyard manure, black soil and coarse sand (2:2:2:1). This mixture was left for periods varying from about 3 months to one year, after which it was again thoroughly mixed and left undisturbed for another 3 months; it was then ready for use.

The day was from sunrise till sunset during summer time; from September till the end of April the day was extended till midnight by means of light supplied by two rows of Philips TL tubes (fluorescent lamps) of 65 Watts each, placed parallel at about 1 metre above a table carrying plants, table width about 1 metre. If in winter daylight was insufficient these TL tubes were lighted. Sometimes mercury vapour lamps were used (Philips HO 450 Watts): one per 4 square metres, placed 1–1.5 metres above the table.

The temperature was kept at 20–22° C, except during the night, when it was lowered to 16–18° C. The relative humidity was about 70 %.

The tobacco, tomato and sugar beet seedlings were grown in seed pans and transplanted in boxes accomodating 100 of them. Here they remained till they were 10 centimetres high, when they were singled out into pots. A few days later the plants were used for tests. Care was taken that all plants included in a test were similar.

With beans the procedure was somewhat different, five seeds being placed in a pot, so that no transplanting was necessary.

As it is known that virus multiplication depends on the age of the host plant, a few details must be added as to the stage of development reached by the test plants before being infected. In all seasons the plants were used for the experiments when the fourth leaf was about 3 cm (4–leaf stage); they were then about 10 centimetres high. In early summer (May–June) sugar beet reaches this stage in about 3 weeks, Rustica tobacco in 4 and White Burley in nearly 5 weeks, bean plants in 2–3 weeks and tomato plants in about 4 weeks. In winter it took them 2–3 months to reach this stage of development.

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[1] Received from the "Koninklijke Beetwortelzaad-Cultuur Kuhn and Co.", Naarden.

[2] Purchased from the "Coöperatieve Aan- en Verkoopvereniging Centraal Bureau Rotterdam".

[3] Purchased from "Turkenburg's Zaadhandel", Bodegraven.

In summer the first visible symptoms of virus yellows in sugar beet appear after about 3 weeks; TMV virus produces symptoms in a little more than one week, the bean viruses and TMV in tomato plants in 1–2 weeks. In winter these periods are 2–3 times longer; with yellow virus in sugar beet only mild symptoms appear, if any.

Generally the winter season is not ideal for these experiments, as certainly the light intensity is a limiting factor and probably also the temperature. To our amazement, for tobacco plants September is too unfavourable for symptoms to be developed.

3. VIRUSES

As explained in Chapter I the viruses and plants were so chosen as to produce diseases having their strongest influence on the production of either leaves, roots or seeds.

The major part of the work was done in the greenhouse with:

a. Tobacco mosaic virus (Nicotiana virus 1) in tobacco; leaf damage.
b. Yellow virus (Beta virus 4) in sugar beet; damage especially to the roots.
c. Common and yellow bean mosaic virus (Phaseolus viruses 1 and 2) in French bean and broad bean; reduction of seed production.

Tobacco mosaic virus (TMV) is very stable. A mixture of a few strains obtained from the Institute for Phytopathological Research (I.P.O.) at Wageningen was investigated. In some cases it was necessary to purify the virus (especially for the methods described under 4), which was done according to the directions of BAWDEN (1950), K. M. SMITH (1951) and THUNG (1949).

Sugar beet yellow virus is rather unstable; it cannot be stored outside the plant, therefore it was not purified. For this investigation a mixture of strains was used, as it seemed desirable to test the antivirus activity of the compounds against several strains available in nature.

The bean viruses isolated lose infectivity within two days (BEEMSTER and VAN DER WANT, 1951; VAN DER WANT, 1954), so that purification is impossible. A mixture of a few strains received from I.P.O. was used.

4. METHODS OF INFECTION

The plants were inoculated with TMV and the bean viruses in the usual way by rubbing the leaves with carborundum powder and injecting them with diluted cell sap. Only one half of the leaf thus treated was inoculated. If the whole leaf should be treated, it might be killed by the inoculum before the virus had become systemic in the plant. The crude TMV sap can be diluted considerably with water without losing its infectivity. Generally, dilutions of 1:1000 and even higher still cause the plants to become diseased, however, only dilutions of about 1:10 were used.

Sugar beet yellow virus cannot be inoculated with this technique. Here the insect vector, *Myzus persicae* (*Sulz.*), had to be used. This aphid was bred on diseased plants throughout the year. To be sure of infection on every plant 10 of such aphids were placed (mostly

6 will be sufficient). Two days later they were killed with an insecticide that had no residual effect.

5. DETERMINATION OF DEGREE OF VIRUS INFECTION IN PLANTS

As a chemotherapeutic compound cannot be expected to suppress virus multiplication altogether in all cases and considering that the virus, once it has become capable of overcoming the chemotherapeutic action, will continue to multiply, the differences between the treated and untreated plants will be greatest in the early phases of the disease. Therefore it was important to determine the degree of virus infection as soon as possible after the anti-virus compound had been applied and infection started.

For all methods described below test and control plants had to be of the same age and stage of development. Often a few leaves were sufficient for a test; these leaves had to be taken from similar parts of the plants included in that test. In those experiments where leaf discs could be used they were neither cut from the small top leaves nor from the oldest bottom leaves; nor were large veins included. This technique was preferred as the plants themselves remained intact and could be used for a further determination.

The following methods were applied:

a. *Serology*

An anti-serum was obtained from rabbits injected intravenously with a purified virus solution. This anti-serum was used to establish, by means of the precipitation reaction, the presence of virus in the purified sap extracted from the plants under test. Equivalent amounts of virus and anti-serum have to be used, as an excess of either of them may inhibit precipitation (prozone effect). For the precipitation reaction a rather impure sap could also be used; the sap extracted from the plants by crushing leaves in a mortar was heated at 60° C for about 10 minutes, after which the bulky green precipitate of plant material was removed by centrifuging.

The agglutination reaction was also performed with crude plant sap. Any virus present in the sap produces agglutination of the anti-serum and the chloroplasts.

Routine serological tests were done to investigate tobacco mosaic virus and yellow virus in sugar beet.

With TMV the following procedure was used:

Anti-serum was obtained by injecting rabbits intravenously with 3–5 ml of a purified virus solution. After 4–8 injections the titer of the anti-serum was usually sufficiently high. Rabbit's blood was then collected and left for some hours to clot. The anti-serum was poured off and centrifuged to remove any blood cells left. It is not sterile and has to be stored frozen.

Infected plant material was crushed and 1 ml of the sap thus obtained was heated for about 10 minutes at 60° C and centrifuged at low speed, i.e. 3000 r.p.m.[1]) The supernatant liquid was stored, if necessary at 0° C. Before use it was diluted with 0.85 % NaCl solutions in ratios of 1:1, 1:4, 1:8, etc., as was also done with the anti-serum.

The bottom of a Petri dish was coated with a hydrophobic film of "Vinylite" (a mixture of polyvinyl acetate and polyvinyl chloride, applied as a 1 % solution in chloroform). With a drawnout pipette a drop of the virus extract was placed on the bottom of the Petri dish, and a drop of anti-serum on the same spot. This was repeated with the dilute virus and the anti-serum dilutions. Besides, a complete set of controls was run with healthy plant sap and normal rabbit serum.

When all drops were in the desired position a paraffinic oil ("Shell Ondina" oil 29 or Oleum paraffinicum) was carefully poured into the dish, until they were just covered, without disturbing them. The dishes were incubated at 37° C for 15 minutes and were then examined for flocculae under the microscope (method described by VAN SLOGTEREN, 1955).

Table II gives an example of a serological determination of the concentration of a virus solution. For various concentrations of the anti-serum the maximum dilutions of TMV in the solution to be tested which still gave a normal serological reaction were determined. This was repeated with a standard virus solution. The ratios of the two dilutions were determined and the mean values calculated (for the relative anti-serum concentrations of 1, $^1/_2$, $^1/_4$, $^1/_8$, $^1/_{16}$ the ratio was 2, 2.5, 1, 1, and 2 for the + signs in the table and 2, 4, 4, 1, and 1.3 for the ± signs).

The concentration of the unknown TMV solution was thus found to be 0.25 %.

The incubation period, i.e. the time interval (in days) between the moment of infection and the appearance of the first symptoms, was at least 16 days for White Burley tobacco in experiments performed in January and February 1954. Serologically, however, it could be demonstrated that the virus was present in the top leaves as soon as 12 days after inoculation. Somewhat later in the season, in March, when the rate of growth increases, the first symptoms of the disease were noticeable after an incubation period of about 10 days and serologically the virus was shown to be present 7 days after inoculation. It may be expected that later in the season this incubation period will be shorter still.

The concentration of TMV in *Nicotiana rustica* is low, the highest found being 0.006 % .The reason for this is that the disease causes a top necrosis resulting in the growing point dying off on account of which the virus multiplication decreases rapidly. Owing to this low concentration it was impossible to obtain exact data on the virus propagation during the incubation time. Often a few days before the end of the incubation time a slight serological reactivity was found.

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[1]) Number times gravity: 1000–1500.

TABLE II

Example of a serological determination of the titer of a TMV solution as compared with a standard TMV solution of 0.1%

The unknown virus solution was isolated from White Burley tobacco plants, purified according to K. M. Smith (1951), Bawden (1950) and Thung (1949). Both the virus extract and the anti-serum (prepared from rabbit's blood) were diluted with 0.85 % NaCl solution. Incubation for precipitation reaction: 15 min. at 37° C. Duplicate determinations were performed as microtests in Petri dishes; for every reaction one drop of anti-serum and one drop of virus solution were mixed. Controls with the physiological salt solution (0.85 % NaCl) did not give precipitations. ++, + = positive serological reaction; ± = just perceptible reaction; 0 = no reaction.

Relative concentr. of anti-serum	Virus solution to be tested														Standard virus solution of 0.1 %													
	Dilutions														Dilutions													
	1 ×		2 ×		4 ×		8 ×		16 ×		32 ×		64 ×		1 ×		2 ×		4 ×		8 ×		16 ×		32 ×		64 ×	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
1/1	++	++	++	++	++	++	+	+	++	+	±	±	0	0	++	++	+	++	++	++	+	+	±	±	0	0	0	0
1/2	++	++	++	++	++	++	++	++	+	+	±	±	0	0	++	++	++	++	++	++	±	+	0	0	0	0	0	0
1/4	++	++	++	++	+	+	±	+	±	+	±	±	0	0	++	++	++	++	++	++	±	+	0	0	0	0	0	0
1/8	++	++	++	++	+	+	±	±	0	0	0	0	0	0	+	+	+	+	+	+	±	±	0	0	0	0	0	0
1/16	++	++	++	++	+	+	±	0	0	±	0	0	0	0	±	±	+	+	±	±	±	±	0	0	0	0	0	0
1/32	±	±	±	±	0	0	0	0	0	0	0	0	0	0	±	±	0	±	0	0	0	0	0	0	0	0	0	0
1/64	0	0	±	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1/128	0	0	±	±	0	0	0	0	0	0	0	0	0	0														
1/256	±	0	±	0	0	0	0	0	0	0	0	0	0	0														
1/512	0	0	0	0	0	0	0	0	0	0	0	0	0	0														

The routine serological test to investigate sugar beet yellow virus was somewhat different. Plant sap from diseased leaves was diluted with its own volume of 0.85 % NaCl solution and centrifuged for 15 minutes at low speed (3000 r.p.m.). The supernatant liquid was stored at 0° C. Before use (usually the next morning) it was once more centrifuged at the same low speed for 15 minutes and diluted further if required.

The anti-serum was obtained from the Laboratory of Bulb Research at Lisse [1]). It had been prepared from the blood of rabbits injected with crude sap. The anti-serum was received frozen-dried in small ampullas. Upon being dissolved in 1 ml 0.85 % NaCl solution it was ready for use.

The experimental procedure was similar to that with TMV, the incubation period of the Petri dishes now being 2–4 hours at 37° C before they could be examined for flocculae under the microscope. Owing to the instability of the sugar beet yellow virus it is not possible to prepare a standardized virus solution. Consequently, the absolute amount of virus present in the host plants treated with a chemotherapeutic compound and in the untreated control plants could not be established and the investigations had to be restricted to determining the ratio of the two values at the end of the experiment.

Beet serology is rather difficult and is more time-consuming than tobacco serology. Although several tests were done it was impossible to demonstrate the presence of the virus earlier than 1–2 days before the end of the incubation period, when the leaves were already somewhat crisp. The distribution of the virus over a plant is rather uneven, as already found by BOOIJ and Coworkers (1944). There are even indications that the distribution of the virus over one leaf is variable.

An objection to these methods of virus determination may be that virus particles may lose their activity, but not their reactivity. It seems fairly certain that the infectivity is localized in the ribonucleic acid part of the particle and not in its protein part, the latter being responsible for the serological reaction (FRAENKEL CONRAD (1955), MATTHEWS and SMITH (1955), MARKHAM (1953), GIERER and SCHRAMM (1956 a and b)).

b. *Reducing sugar test according to* VAN DUUREN (1955)

This is a rough test for the presence of yellow virus in sugar beet. When the plants are infected the transport of metabolites to the roots is disturbed, which leads to a surplus of reducing sugars in the leaves. This could be determined by punching, preferably in the morning, a disc of 6 millimetres diameter from the central interveinal tissue of four outer leaves of a plant. These four discs were placed in a tube containing 4.5 ml water and 0.5 ml of a 0.5 % solution of 3.5-dinitrosalicylic acid in 1 N sodium hydroxide. Several of such samples were kept at 100° C in a water bath for 30 minutes. Immediately after cooling optical density readings were taken at 500 mμ with a spectrophotometer, the transmission of the control tube without plant material being adjusted at 0. The colour was not stable and had to be measured within 2 hours.

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[1]) The author wishes to express his thanks to Professor Van Slogteren and his collaborators for supplying this anti-serum.

The optical density values with young healthy leaves was nearly zero: with older uninfected leaves from greenhouse plants they were somewhat higher, but always less than 0.13. With mature leaves from field-grown sugar beet plants even higher values may be found. Leaves with symptoms of infection gave optical densities higher than 0.23. Values between 0.13 and 0.23 were difficult to interpret; they probably refer to infected leaves in the incubation period.

In Table III an example of this test is given.

TABLE III

Van Duuren test on sugar beet yellow virus

Every sample consists of 4 discs (dia. 6 mm) punched from outer leaves. It is placed in a tube containing 4.5 ml water and 0.5 ml of a 0.5% solution of 3.5-dinitrosalicylic acid in 1 N sodium hydroxide; the tube is kept in a water bath of 100° C for 30 minutes.

Plant material	Days after infection	Incubation time, days	Optical density at 500 mμ
Normal healthy plants	0	0	0.08; 0.10; 0.11; 0.11
Infected plants			
a. during incubation period	18	24, 25	0.09; 0.12; 0.18; 0.32
b. after incubation period	22, 44	21, 21	0.35; 0.41; 0.46; 0.96

c. *Reso blue test*

This test, introduced by Igel and Lange to determine leaf roll virus in potatoes, is described by MÜNSTER (1955) and SCHUSTER (1956). It demonstrates callus formation by a blue colouration in the phloem. Diseased plants form more callus than healthy ones. The same holds for sugar beet plants affected by virus yellows. Sections (1–2 millimetres thick) from the hypocotyl of a sugar beet plant were dipped in a reso blue [1]) solution (100 mg/l) for 3 minutes, after which they were immersed in a 1 % $CaCl_2$ solution to fix the dye. The microscope revealed blue callus stains 10–80 μ long and about 15 μ broad in the phloem. It was simple enough to distinguish severely diseased from healthy material, judging by the amount of callus formed. It proved to be difficult, however, to decide on the presence of virus during the incubation period. The results obtained in that period were often unreliable. The uneven distribution of the callus in the sections provided another difficulty. Therefore the selectivity of this test was not high. BROADBENT and HEATHCOTE (1957) came to the same conclusion when they used this method to investigate leaf roll virus in potatoes.

d. 2, 3, 5-*triphenyl tetrazolium chloride* (*TTC*) *test*

According to F. E. SMITH (1951) the insoluble red triphenyl formazone is formed in the colourless solution of TTC in the presence of tissue by the following reaction:

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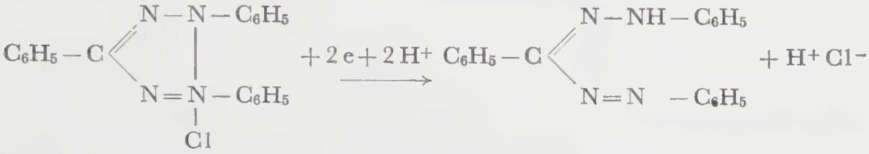
[1]) Supplied by E. Gurr, Germany.



$$C_6H_5-C\begin{array}{l}N-N-C_6H_5\\ \quad\;\; |\\ N=N-C_6H_5\\ \quad\;\; |\\ \quad\; Cl\end{array} + 2e + 2H^+ \longrightarrow C_6H_5-C\begin{array}{l}N-NH-C_6H_5\\ \\ N=N-C_6H_5\end{array} + H^+Cl^-$$

The TTC acting as an electron acceptor for many pyridine nucleotide dehydrogenases. In 1955 BEAL and Coworkers used TTC to detect the presence of viruses in plants. In virus-infected tissue (roots, stems, petioles or leaves) a relatively rapid change in colour from colourless via green, rust and amber to red occurs, whereas in virus-free tissue a similar but much slower change can be observed.

The maximum differences were usually observed at 35° C within 15–30 minutes after the sections had been immersed in $1\frac{1}{2}$–2 ml of a $0.1^0/_0$ aqueous solution. In the experiments described below, however, the reaction was performed at low pressure (9 centimetres Hg) in order to evacuate the air from the plant tissue, owing to which it sinks. As tissue five leaf discs of 6 millimetres diameter were used. Contrary to the common view it is of great advantage to note, not the colour changes of the sunken tissue itself, but those of the solution, as in the medium the reaction proceeds at a much lower rate. The discs need about 20–30 hours to sink. This is done in the dark; afterwards they are placed in daylight and the vacuum is removed. The colour change can be measured spectrophotometrically at 550 mμ within 10 hours.

Leaf discs from healthy plants impart a red colour to the solution, while discs from diseased plants which have had symptoms for some time give a pink colour. Leaf discs examined during incubation

TABLE IV

TTC (2, 3, 5-triphenyltetrazolium chloride) test on yellow virus in sugar beet and on TMV in tobacco (White Burley)

For each test 5 leaf discs of 6 millimetres diameter were used. They were placed in a 0.1 % solution of TTC at low pressure (9 cm Hg). About 48 hours later the change in colour was measured.

Plant material	Days after infection	Incubation time, days	Optical density at 550 mμ
Normal healthy sugar beet plants	0	0	0.36; 0.29; 0.25
Infected sugar beet plants			
I. during incubation period	8, 16, 18	20, 21, 20	0.26; 0.60; 0.51
b. after incubation period	19, 23, 19	18, 20, 19	0.23; 0.24; 0.24
Normal healthy tobacco plants	0	0	0.36; 0.35; 0.41
Infected tobacco plants			
a. during incubation period	2, 4, 4	7, 7, 6	0.40; 0.48; 0.59
b. after incubation period	14, 12, 10	7, 8, 7	0.44; 0.59; 0.54

produce a darker red colour of the solution than healthy ones. Table IV gives the corresponding optical density values.[1])

e. *Determination of plant (tissue) respiration according to* Blom *and* Edelhausen (1955)

With the aid of an improved spectroscopic method Owen (1955a, b, 1956, 1957a, b) determined the respiration rate of tobacco plants infected with TMV, especially during the incubation period. In leaves the respiration rate increased within an hour after inoculation, being considerably higher than in the uninfected control plants. When the plants showed visible symptoms and the leaves contained the maximum amount of virus the respiration rate fell below that of the controls. As the increase in respiration rate started shortly after the leaves had been inoculated, long before virus multiplication was detectable by serology or by the glutinosa test, it was investigated whether this rate could be determined according to the method of direct CO_2 titration as described by Blom and Edelhausen (1955). This method is based on the relatively great solubility of CO_2 in acetone. The CO_2 production of plants was determined in the following way.

Through a closed container, in which plant material was kept in the dark, CO_2 free air was passed for a certain period of time and, together with the CO_2 produced by the plant, was led into acetone. The volume of air thus passed through was measured with a flow meter. The amount of CO_2 entrained was determined by titrating the CO_2 absorbed by the acetone with a 0.01 or 0.1 N solution of sodium methanolate (CH_3ONa) in methanol, thymol blue being used as the indicator.

Although this method was found to be not very reliable, indications were obtained that during the incubation time White Burley plants have a higher respiration rate than uninoculated plants. When after the incubation time the diseased plants have distinct symptoms, their respiration rate is probably less than that of healthy plants. The same seems to be true for sugar beet plants, although not to such a pronounced degree.

f. *Nicotiana glutinosa test*

To determine the amount of TMV some infected material was passed through a mincer and the sap used for inoculating one half of leaves of healthy *Nicotiana glutinosa* plants, the other halves being inoculated with a standard TMV solution of known virus content. The number of local lesions formed after a few days was counted. The content of tobacco mosaic virus can be determined by comparing the number of local lesions in the test half of the leaf with that of the control half.

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[1]) As it is difficult to prepare uniform samples from discs an improvement was made later on by using plant sap after centrifuging at 7000 r.p.m. during 25 minutes. Also it is better to keep the reaction continuously in the dark as a TTC solution is light-sensitive.

However, the results are influenced by the age of the *Nicotiana glutinosa* leaves and, moreover, by the fact that these leaves are not uniform in shape and size; besides, it is impossible to calculate exactly the virus content in the plant if only a small part of this plant is used as test material.

Testing chemicals for their chemotherapeutic activity on *Nicotiana glutinosa* has the drawback that this compound has to act merely on the spot where virus penetrates into the plant. Consequently, its action on a virus causing local lesions must be more vigorous than on a systemic virus.

It must be pointed out that none of these methods is entirely trustworthy. Therefore, in investigating the chemotherapeutic effect of various compounds all the methods mentioned above were applied. As it proved to be too time-consuming to examine the whole range of compounds in this way, only those were tested further which influenced the virus multiplication at least in such a way that the visible symptoms became less distinct. It must be remarked, however, that the seriousness of the symptoms does not always correlate with the amount of virus present, as COONS (1954) described for virus yellows in sugar beet.

A chemotherapeutic effect was considered positive only when the results of all the tests mentioned were in agreement.

6. APPLICATION OF COMPOUNDS EXPECTED TO HAVE CHEMOTHERAPEUTIC ACTIVITY

The chemicals to be tested were always applied before infection took place, either by spraying the leaves or through absorption of a solution via the roots.

a. *Spraying*

Fifty mg of the chemical to be tested was dissolved in 50 ml water, or, in several instances, in 2 ml acetone containing 0.1 % Triton X 155¹) as wetting agent and poured into 48 ml water. The plants, placed in an area of 0.5 square metre, were evenly sprayed with this solution at 3 atmospheres in high volume (50 ml/0.5 square metre is 1000 litres/hectare). The same number of control plants were sprayed with water containing acetone and wetting agent.

Two days after spraying the plants were inoculated with the exception of a number of them, which was the same in the two sets of plants. Thereupon, if the results were promising the plants were examined by the methods just described, either once more during the incubation time or at the end of this period. Compounds which showed no chemotherapeutic activity in a 0.1 % w solution were considered to have no anti-virus properties. If a 0.1 % w solution appeared to have a phytotoxic effect on the uninfected control plants lower concentrations were tested.

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¹) Rohm and Haas, USA.

b. *Absorption via the roots*

The compound enters the plant through the roots and is transported to the leaves and the upper growing point.

Healthy plants were lifted from their pots. Their roots with adhering soil were kept in an 0.1 % w aqueous solution (mostly without acetone and wetting agent) for 24 hours. Subsequently they were potted up again and 24 hours later were inoculated with the virus. This is called the dipping method. As to the controls the same precautions were taken as with the spraying technique.

In modern practice nursery plants are often transplanted with so-called "soil blocks"; in this case the dipping method may be of more practical value than the spraying treatment.

A drawback of the dipping method is that an unknown, maybe sometimes large, quantity of the substance is absorbed by the adhering soil, which may delay the absorption by the plant to a point of time too late to prevent virus multiplication.

To prevent this disturbing effect the plants, after having germinated, were transplanted in 1½–2 kilogrammes of sterilized sand in red plastic "Vinidur" boxes (20 × 20 × 10 centimetres; the red colour was chosen because it contrasts well with the plant material). The roots of the test plants were rinsed with tap water; 8 plants were planted in each box. Then the chemical under test was added, in a concentration of 0.001–0.01 % w, to 150–200 ml of Knopp's solution and with this mixture the sand was wetted evenly (nutrient technique). Usually two days later six plants were inoculated with the virus in the common way, the other two remaining uninfected. The controls were the same as with the spraying technique.

III. EXAMINATION OF ANTI-VIRUS SUBSTANCES IN THE GREENHOUSE

1. Literature

A compound will be regarded as an antivirus factor when, upon penetrating into the plant tissue, it can inactivate the virus in vivo or inhibit the virus multiplication; besides, it must not produce a phytotoxic effect in the concentration used.

In Table V a survey is given of the various antivirus compounds (column 1) mentioned in the literature (column 5).

The concentrations used are not recorded; they were always low, varying from 0.001 %–1 %. In columns 2 and 3 the plants and viruses are recorded on which the influence of the chemotherapeutic was investigated; it can also be found when the local lesion method was used to determine the degree of activity (TMV with as host plant *Nicotiana glutinosa* or bean, Southern bean mosaic virus and its host Pinto bean). As pointed out on page 377 this method has serious drawbacks as an in vivo test.

Sometimes it is not clear whether an inhibitor activity is described or whether the compound displays real, i.e. in vivo antivirus activity. Therefore in column 4 of the table the methods used to apply the compounds are indicated.

TABLE V

Antivirus compounds mentioned in the literature

Method: 1. absorption of the chemotherapeutic substances through the root system; — 2. vacuum infiltration, mostly of the leaves; — 3. spraying; — 4. floating the detached leaves or leaf discs on the solution of the chemical under test, whether or not solidified with agar; — 5. wrapping a cotton pad drenched with the compound round the shoots; applying the chemical at a certain spot of the plant in a lanoline paste, or through a woollen thread passed into the stem; dipping an intact bud or leaf in a solution of the compound for a certain time; injecting the plants with the chemical, etc.; — 6. treatment of the seeds, seed potatoes or beet stecklings with a solution of the compound; — 7. tissue cultures, the compound added to the tissue nutrient solution.

Compound	Virus	Host plant	Method	Author(s)
Thiouracil	TMV	tobacco	4	Commoner, Mercer (1951)
			3	Mercer, Lindhorst, Commoner (1953)
			1, 4	Nichols (1953; 1954)
			4	Jeener, Rosseels (1953)
			4	Schlegel, Rawlins (1953; 1954*b*)
			1	Holmes (1954; 1955)
	lucerne mosaic virus	tobacco	1, 3	Matthews (1953)
		beans		
	TMV	tobacco spp.	3, 4	Bawden, Kassanis (1954)
	several other viruses	several other plants		Bawden (1954)
	stone fruit virus	cucumber	2	Kirkpatrick, Lindner (1954)
	TMV	tomato		
	ring spot virus	plum tree	5	Milikan, Guengerich (1957)
	cucumber mosaic virus	tobacco	1	Porter, Weinstein (1957)
guanazolo (8-azaguanine)	lucerne mosaic virus	clover	1, 3	Matthews (1951; 1952; 1953*a*, *b*; 1954)
	TMV	tobacco (also Nic. glutinosa)		
		tomato		
	stone fruit virus	cucumber	2	Kirkpatrick, Lindner (1954)
	TMV	tomato		
	virus yellows	sugar beet	1, 3	Russel, Trim (1957)
	ring spot virus	plum tree	5	Milikan, Guengerich (1957)

TABLE V (continued)

Compound	Virus	Host plant	Method	Author(s)
guanazolo (8-azaguanine)	TMV	tobacco	3	Mercer, Lindhorst, Commoner (1953)
2-thiocytosine 2-thiothymine 2.6-diaminopurine 6-methylpurine 6-chloropurine	TMV	tobacco	7	Kurtzman and Coworkers (1957*a*, *b*)
pyrimidines thiazole malonic acid nicotinic acid	TMV	tobacco	4	Ryzhkov, Marchenko (1954, 1955)
diazouracil dl- and l-isoleucine several other chemicals	TMV	tobacco	4	Schlegel, Rawlins (1953; 1954*b*)
malachite green	TMV	tobacco	4	Takahashi (1948; 1957)
	TMV	tomato	3	Williams and Coworkers (1952)
	potato virus X potato virus X	potato var. Green Mountain (Early Carmen)	7	Norris (1954, 1955*a*, *b*)
malachite green other triphenylmethane dyes, as: victoria blue, night blue	TMV	tobacco	4?	Kausche, Hahn, Schleith (1950)
methylene blue crystal violet malachite green neutral red	tissue tumour virus 1)	Rumex acetosa	7	Nickell (1951)
chloramphenicol	stone fruit virus TMV	cucumber tomato	2	Kirkpatrick, Lindner (1954)
naphthalene acetic acid	tissue tumour virus 1)	Rumex acetosa	7	Nickell (1950)
	TMV	tobacco	7	Hildebrandt, Riker, Watertor (1952)
			3	Nichols (1952*a*, *b*)
	lettuce big-vein virus	lettuce seedlings	1	Rich (1954)

coconut milk	TMV	tobacco	7	Segretain, Hirth (1956)
aspartic acid				
glutamic acid				
2,4-dichlorophenoxy acetic acid	TMV	tobacco	7	Van Overbeek (1952)
methoxine				
naphthalene acetic acid				
2,4-dichlorophenoxy acetic acid	chrysanthemum mosaic virus	chrysanthemum	1	Howles (1953; 1955)
2,4,6-trichlorophenoxy acetic acid	lettuce big vein virus	lettuce seedlings	1	Rich (1954)
indole acetic acid				
ammonium salt of 2,4-dichlorophenoxy acetic acid	TMV	tobacco	1, 3, 6	Howles (1957)
	tomato aspermy virus	chrysanthemum		
3-chlorophenoxy acetic acid				
cortisone	TMV	tobacco	4	Hirth, Stolkowski (1957)
calcium chloride	carnation mosaic virus	carnation	5	Thomas, Baker (1950)
			1, 3	Rumley, Thomas (1951)
	lettuce big vein virus	lettuce seedlings	1	Rich (1954)
potassium bromide	TMV	tobacco	1	Sardina (1951, 1953)
sodium bromide			1	Cordon (1953)
ammonium bromide				
sodium chloride	potato virus X	seed potatoes	6	Kanngiesser, Deubner (1954)
potassium chloride				
trisodium phosphate	TMV	tomato seed	6	John, Sova (1956)
sodium hydroxide	TMV	tomato seed	6	Milinko (1956)
	cucumber mosaic virus			
mineral salts	TMV	Pinto bean	1, 6	Panzer (1957)
zinc	TMV	tobacco	1, 4	Helms, Pound (1955)
zinc sulphate	peach X virus	peach tree	5	Stoddard (1944)
	carnation mosaic virus	carnation	1, 3	Rumley, Thomas (1951)
	lettuce big vein virus	lettuce seedlings	1	Rich (1954)
zinc chloride	TMV	tobacco	4	Schlegel, Rawlins (1953; 1954*b*)
zinc chloride	TMV	tobacco	4	Weintraub, Gilpatrick, Willison (1952)
zinc sulphate	carnation mosaic virus	Dianthus barbatus		
	strawberry virus 2	strawberry	1	Fulton (1954)
nitrous acid (HNO_2)	TMV	tobacco	5	Kasahara, Kakumizu (1953)
milk	TMV	tomato	3	Anonymus (Bawden, 1954*a*, *b*)

[1] tissue tumour virus Aureogenus magnivena Black.

TABLE V (continued)

Compound	Virus	Host plant	Method	Author(s)
trichothecin	TMV	tobacco	3, 4	Bawden (1954)
ribonuclease	TMV	tobacco	2	Casterman, Jeener (1955, 1956)
4-chloro-3,5-dimethylphenoxy-ethanol	TMV	tobacco	1	Davis (1952)
tannic acid	TMV	tomato	3	Williams and Coworkers (1951)
streptomycine	TMV	tobacco	4	Leben, Fulton (1952; 1953)
	necrosis virus	cow pea		
	ring spot virus	cow pea		
vitamin B 1	TMV	tobacco Nic. glutinosa	4	Weintraub, Gilpatrick, Willison (1952)
MK 61 (antibiotic from Nocordia species)	TMV	tobacco	4	Schlegel, Rawlins (1954*a*)
noformicin (antibiotic)	TMV	tobacco	1, 3	Gray (1955)
	Southern bean mosaic virus	Pinto bean		
cytovirin (antibiotic)	TMV	tobacco	1, 3	Gray (1957)
	Southern bean mosaic virus	Pinto bean		
quinhydrones 8-hydroxyquinoline calcium hydroxyquinoline magnesium hydroxyquinoline o-nitrophenol urea sodium thiosulphate	peach X virus	peach tree	5	Stoddard (1942)
p-aminobenzene-sulphanylamide do. mixed with maltose or dextrose p-toluenesulphanylamide hydroquinone	peach X virus	peach tree	5	Stoddard (1944)

sulphathalidine sulphamerizine p-aminobenzenesulphoxylamide sodium diethyldithiocarbamate				
hydroxyquinoline sulphate sulphathiazole sulphaguanidine sulphasuxidine sulphathalicidine sulphamerizine	carnation mosaic virus	carnation	1, 3	Rumley, Thomas (1951)
ethanol containing crotonaldehyde and possibly small quantities of other aldehydes, higher alcohols and/or methanol and/or pyridine bases	several viruses	several plants	1, 3	Nyman (1952)
sodium salt of 4-sulphonamidephenyl azo-7-acetylamino-1-oxynaphthaline 3,6-disulphonic acid (= prontosil)	TMV	tobacco	1	Sardina (1951; 1953)
radiophosphorus P_{32}	TMV	tobacco	4	Schlegel, Gold, Rawlins (1953)
furfuryl-5-chloro-2-methyl carbanilate furfuryl carbanilate	Southern bean mosaic virus	Pinto bean	5	Porter and Coworkers (1957)
nemagon carbon bisulphide methyl bromide DD mixture Vapam	peach yellow bud mosaic virus	peach tree	1	Wagon, Traylor (1957)

MATTHEWS and SMITH (1955) and ROLAND (1955) have given reviewing articles on this subject; WEINTRAUB and KEMP (1955), who investigated Nicotiana glutinosa, and SCHLEGEL and RAWLINS (1953; 1954 a, b) who applied the leaf disc technique, have given extensive lists of all chemicals screened by them.

It appears that most investigations have been done with 2-thiouracil, guanazolo, the triphenylmethane dyes (malachite green), growth substances, and inorganic nickel, zinc and calcium salts. The other compounds mentioned have scarcely been examined and it seems desirable to verify their activity by more research.

2-Thiouracil, a representative of the pyrimidines, is first described as an antivirus factor by COMMONER and MERCER (1951); they used TMV in tobacco with the leaf disc method. Antivirus activity was found at concentrations of down to $4.3 . 10^{-5}$ mols per litre. According to these authors thiouracil is incorporated in the virus particle where it replaces uracil and inhibits virus propagation. The same view is held by JEENER and ROSSEELS (1953), who worked with ^{32}S labelled thiouracil, by MATTHEWS (1953 a, b; 1954), and by MATTHEWS and SMITH (1955). The first-mentioned authors were able to trace the radio-activity in the virus particle. NICHOLS (1953) also accepts this view, but he points out that this substance is phytotoxic, as it causes chlorosis of the plant and thus inhibits virus multiplication.

PORTER and WEINSTEIN (1957) also stress the harmful effect (interveinal chlorosis) of thiouracil on the plants and point out the antimetabolic relationship between thiouracil and uracil.

The antivirus activity of guanazolo (8-azaguanine or 5-amino-7-hydroxy-1-V-triazolo(d)-pyrimidine) and related compounds mainly towards lucerne mosaic virus and TMV, obtained by spraying white clover or tobacco plants, or drenching the soil in which these plants grow, with concentrations up to 1 % is mainly described by MATTHEWS (1951, 1953 b, 1954) and by MATTHEWS and SMITH (1955). MATTHEWS states that guanazolo had already been described as a strong inhibitor of the growth of microorganisms (see also CHANTRENNE and DEVREUX (1958)), fungi and algae, and of virus tumours (NICKELL and Coworkers (1950), CHANTRENNE and DEVREUX (1958)), even of malignant cells in mice. It was suggested that the growth inhibiting effect should be attributed to the interference of guanazolo with the incorporation of guanine in the nucleic acids. A similar conclusion was drawn from the experiments on the effect of guanazolo on the reproduction of lucerne mosaic virus; 3-4 % of the guanine in the virus nucleic acid was replaced by 8-azaguanine. This incorporation reduced the infectivity of the virus.

Other investigators (BAWDEN (1954); RUSSEL and TRIM (1957)) do not sustain this theory, as both thiouracil and 8-azaguanine have a marked phytocidal effect. As these compounds affect the metabolism of plants enough to change their appearance there is, according to BAWDEN (1954), obvious reason to suppose that they inhibit virus multiplication by affecting some host-cell mechanism rather than by acting directly on the virus particle.

The activity of the triphenylmethane dye malachite green was first mentioned by TAKAHASHI (1948). He floated tobacco leaves inoculated with TMV on malachite green solutions and observed that in concentrations as low as 2 ppm the virus synthesis was inhibited. He suggested that the compound acts as a block in enzyme reactions, leading to virus formation, but it was already known that malachite green inhibits the activity of a dehydrogenase in *Escherichia coli* and also affects the respiration of tobacco stem tissue. Its technical use is hampered by its very poor penetration ability. Malachite green also greatly reduces intercellular growth of influenza virus and it is suggested that this effect may be due to interference with ribonucleic acid metabolism (HOYLE, 1951).

Besides, it is known from the work of BRAUN (1951), RYZHKOV and Coworker (1950) and KAUSCHE and Coworkers (1950) that triphenylmethane dyes react with proteins, particularly with the nucleoproteins of TMV in vitro. In particular, an inactivating effect was found for alkaline triphenylmethane dyes.

The chemotherapeutic activity of the growth substances is difficult to interpret, because HARTMAN and PRICE (1950) even found that under certain circumstances growth regulators of the 3-naphthoxy acetic acid group increased Southern bean mosaic virus synthesis in Pinto bean.

The antivirus activity of nickel, zinc and calcium salts has been investigated by several research workers, but has not been explained satisfactorily either.

2. COMPOUNDS TESTED FOR CHEMOTHERAPEUTIC ACTIVITY

Several chemicals were examined in order to determine their antivirus activity. A choice was made from the most important compounds mentioned in Table V and related substances; in addition, benzimidazoles, thiourea derivatives, sulphanilamides and nitroso compounds were included in the investigation. In the group of the nitroso compounds antivirus activity could fairly soon be demonstrated with p-nitroso-dimethyl-aniline on all plants used. This was an incentive to examine a series of this type of compounds. A survey of all the compounds tested for their chemotherapeutic activity is given in Table VI.

In order to obtain a rough measure of the chemotherapeutic effect the incubation periods of the virus-infected plants, both with and without application of the compound under test, were determined. From these two values the percentage change of the incubation period brought about by the compound was calculated. This was done for all the virus-host plant relations tested. Each experiment was repeated at least 3 times in the summer season, care being taken that the various virus-host plant relations participated in the calculations of the average in the same ratio. Thus, this procedure provided a sound basis for estimating chemotherapeutic potency. It is true that this average value does not make the best possible use of the information available, as it ignores the specific differences in effect of a compound

TABLE VI

Compounds tested for their chemotherapeutic activity

Virus-host relations investigated: sugar beet yellow virus—sugar beet; TMV—tobacco (White Burley, no. 11, *Nicotiana glutinosa*); TMV—tomato; Phaseolus virus 1—French bean; Phaseolus virus 2—broad bean.

The compounds were applied according to the methods described on pages 377 and 378 in a 0.1 % solution for spraying and dipping and in a 0.001 % to 0.01 % solution for the nutrient technique (with and without 0.04–0.4 % acetone and wetting agent). The plants were infected with the virus 2–3 days after they had been treated with the compound.

The incubation periods of the virus-infected plants, both with and without application of the compound tested, were determined. From these two values the percentage change of the incubation period brought about by this compound was calculated. This was done for all the virus-host plant relations tested; each experiment was repeated at least three times in the course of 1–3 years. The average values of these percentage changes are given in column 3.

The phytotoxicity of the compounds was roughly reduced from the observed injurious effects and the retarded growth of the treated, non-infected plants as compared with the untreated controls.

++: marked, +: mild, and —: no phytotoxicity. (see column 4)

A. Compounds with chemotherapeutic activity

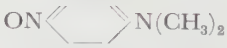
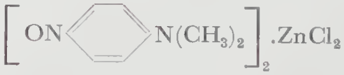
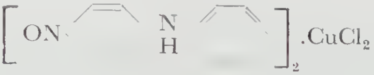
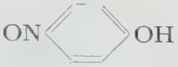
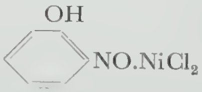
Compound	Chemical structure	Chemo-therapeutic activity	Phyto-toxicity
a. *Nitroso compounds*			
1. *Nitrosoaminoaryl compounds*			
p-nitrosodimethylaniline		10	++
— .HCl salt	— .HCl	10	+
— $.H_3PO_4$ salt	— $.H_3PO_4$	10	—
— $.ZnCl_2$ complex		8	—
— $.CoCl_2$ complex	[—]$_2.CoCl_2$	7	—
— $.H_4Fe(CN)_6$ complex	[—]$_2.H_4Fe(CN)_6$	4	+
— $.Ni(ClO_4)_2$ complex	[—]$_4.Ni(ClO_4)_2$	3	—
p-nitrosodiphenylamine $.CuCl_2$ complex		8	—
2. *Nitrosohydroxyaryl compounds*			
p-nitrosophenol		13	—
— $.NiCl_2$ complex	— $.NiCl_2$	7	—
o-nitrosophenol $.NiCl_2$ complex		15	—
— $.CuSO_4$ complex	— $.CuSO_4$	8	+
— $.ZnSO_4$ complex	— $.ZnSO_4$	7	—

TABLE VI (continued)

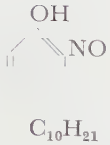
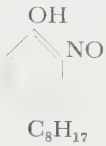
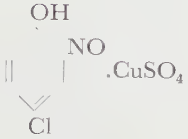
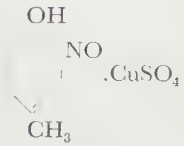
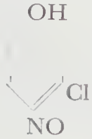
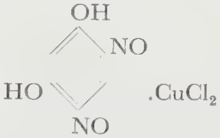
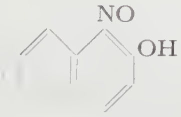
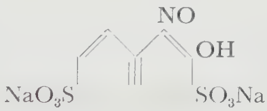
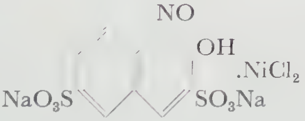
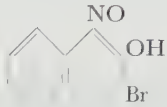
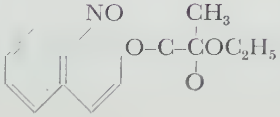
Compound	Chemical structure	Chemo-therapeutic activity	Phyto-toxicity
o-nitroso-p-sec-cetylphenol		4	-
o-nitroso-p-sec-octylphenol		2	—
o-nitroso-p-chlorophenol .$CuSO_4$ complex		12	—
o-nitroso-p-cresol .$CuSO_4$ complex		4	—
m-chloro-p-nitrosophenol		4	+
dinitrosoresorcinol .$CuCl_2$ complex		3	—
1-nitroso-2-naphthol		13	—
— .$NiCl_2$ complex	— .$NiCl_2$	7	—
1-nitroso-2-naphthol-3,6-disulphonic acid (Na salt)		13	+
1-nitroso-2-naphthol-3,6-disulphonic acid .$NiCl_2$ complex		6	—
1-nitroso-3-bromo-2-naphthol		3	+
1-nitroso-2-(1-carboxyethyl)ethoxynaphthalene		5	—

TABLE VI (continued)

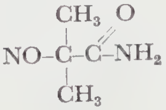
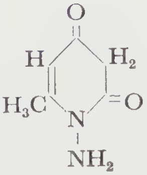
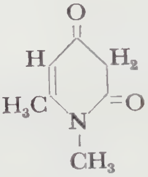
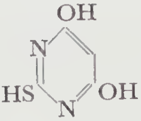
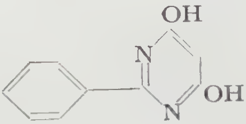
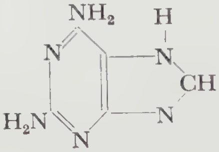
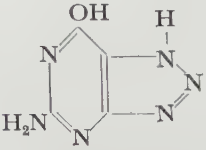
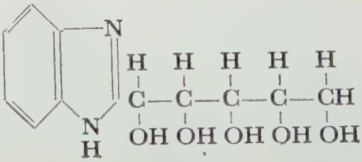
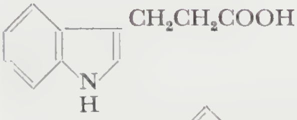
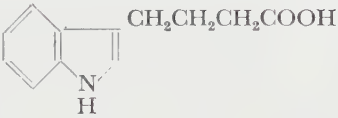
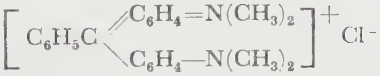
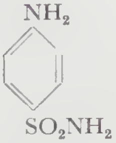
Compound	Chemical structure	Chemo-therapeutic activity	Phyto-toxicity
3. *Other types of nitroso compounds* α-nitrosoisobutyric amide	 $NO-C(CH_3)_2-C(=O)-NH_2$	6	+
b. *Pyridones*			
1-amino-4-oxy-6-methylpyridone		4	—
1,6-dimethyl-4-oxypyridone		4	—
c. *Pyrimidines*			
2-thiouracil		>10	++
2-phenyl-4,6-dihydroxypyrimidine		4	+
2,4-diaminopurine		3	+
8-azaguanine (guanozolo)		4	+
d. *Benzimidazoles*			
1-(benzimidazole-2)-1,2,3,4,5-pentahydroxypentane		3	—

TABLE VI (continued)

Compound	Chemical structure	Chemo-therapeutic activity	Phyto-toxicity
. *Indole derivatives*			
β-(3-indolyl)propionic acid		3	—
γ-(3-indolyl)butyric acid		4	—
Dyes			
malachite green	 $\left[C_6H_5C\begin{matrix}\diagup C_6H_4{=}N(CH_3)_2\\ \diagdown C_6H_4{-}N(CH_3)_2\end{matrix}\right]^{+}Cl^{-}$	8	+
. *Sulphanilamides*			
Sulphanilamide		7	+
. *Inorganic compounds*			
zinc chloride	$ZnCl_2$	7	—
zinc sulphate	$ZnSO_4$	7	—
nickel chloride	$NiCl_2$	8	—

. COMPOUNDS LACKING CHEMOTHERAPEUTIC ACTIVITY

itroso compounds

. *Nitrosoaminoaryl compounds*
p-nitrosodimethylaniline.$CdCl_2$, $MgCl_2$, $FeCl_2$, $CuCl_2$ or urea complexes; p-nitrosomonomethylaniline, p-nitrosodiphenylamine, p-nitroso-N-cyclohexyl-N-ethyl-aniline, p-nitrosotriphenylamine, N-nitroso-N-methylaniline, potassium salt of phenylnitrosoamine, 4-nitroso-1-naphthylamine sulphate, 1-nitroso-2-naphthylamine, p-nitrosodimethylamine, p-chloronitrosobenzene, methylphenyl-N-nitrosoamine.

. *Nitrosohydroxyaryl compounds*
1 hydroxy-2-methyl-4-nitrosobenzene, 1-hydroxy-3-methyl-4-nitrosobenzene, 2,5-dinitrosoresorcinol, 5-nitroso-2-oxydiphenyl, 1-nitroso-4-naphthol, 2-nitroso-1-naphthol, 1-nitroso-6-methylnaphthol-2, 5-nitroso-8-hydroxyquinoline, 2-nitrosophenol, 5-nitroso-1-naphthol, 2-nitroso-5-chlorophenol and its copper chloride complex, 2,4-dichloro-6-nitrosophenol, 1-nitroso-3-chloro-2-naphthol, 8-nitroso-1-naphthol, 8-nitroso-2-naphthol, 5-nitroso-2-naphthol, 2-bromo-4-nitrosophenol, 2-chloro-4-nitrosophenol, acetylated 1-nitroso-2-naphthol, acetylated 1-nitroso-4-naphthol, 1-nitroso-2-naphthol and its copper chloride complex, nitrosoorthocresol, nitrosometacresol.

. *Heterocyclic N-nitroso compounds*
N-nitrosopiperidine, N-nitrosomorpholine.

. *Other types of nitroso compounds*
Potassium salt of nitrosoformamidoxine, α-nitrosoisobutyroamidine hydrochloride, N-nitrosomethylurethane, m-nitrosotoluol, nitrosation product of diphenylether, nitroso-p-ethoxyacetophenone, nitrososalicylic aldehyde and its copper chloride complex, 4-nitrososalicylic acid and its copper chloride complex.

on the various virus-host plant systems. However, it is of practical use, the more so as a large number of virus-host plant relations are concerned.

Compounds with a marked chemotherapeutic activity (arranged in order of decreasing activity) are:
o-nitrosophenol.$NiCl_2$ complex, 1-nitroso-2-naphthol, p-nitroso-phenol, 1-nitroso-2-naphthol-3,6-disulphonic acid (sodium salt), o-nitroso-p-chlorophenol.$CuSO_4$ complex, 2-thiouracil, p-nitroso-dimethylaniline, p-nitrosodimethylaniline.HCl salt, p-nitroso-dimethylaniline.H_3PO_4 salt, p-nitrosodimethylaniline.$ZnCl_2$ complex, p-nitrosodiphenylamine. $CuCl_2$ complex, o-nitrosophenol.$CuSO_4$ complex, malachite green, nickel chloride, p-nitrosodimethylaniline.$COCl_2$ complex, p-nitroso-phenol.$NiCl_2$ complex, o-nitrosophenol.$ZnSO_4$ complex, 1-nitroso-2-naphthol. $NiCl_2$ complex, sulphanilamide, zinc chloride, zinc sulphate, 1-nitroso-2-naphthol-3,6-disulphonic acid (sodium salt). $NiCl_2$ complex, and α-nitrosoisobutyric amide.

One of the most active antivirus compounds so far investigated is p-nitrosophenol. m-Nitrosophenol, on the other hand, had no activity at all. As o-nitrosophenol could not be used owing to its instability its metal salts were examined. It could be demonstrated that especially its nickel salt had an attractive chemotherapeutic activity. *Nicotiana rustica* plants treated with this salt and, two days later, inoculated with TMV did not develop any symptoms of the disease. These plants did not contain the virus in an amount that could be detected serologically. Unfortunately, in further experiments it appeared that these metal salts of o-nitrosophenol are still too unstable to expect that they will be of any use in practice. Therefore, their activity was not further investigated.

The active nitroso compounds are poorly soluble in water; it was investigated whether this could be improved by solving 50 milligrams of the chemical in 2 millilitres of acetone mixed with 0.01 % Triton X 155, as already described in II 6a. This procedure gave a better result. Alcohol could not be used as a solvent on account of its harmful effect. 1-Nitroso-2-naphthol proved to be better soluble in the form of its sodium or potassium salt. without losing its anti-virus activity.

It was tried to improve the formulation by adding: ethyl acetate, dioctyl phosphate, trichloropropane, some paraffinic oils, orthoboric acid, glucose, potassium or sodium hydrocarbonate or sodium phthalate, alkaline sulphite, T-pol or Triton X 155, but of these only Triton X 155 had a favourable effect. This detergent improves spreading and wetting of the plant without being phytotoxic.

The compounds tested differ widely in phytotoxicity. Those having marked phytotoxic properties, such as thiouracil, had to be excluded from further investigations, as they would be of no importance for practical use.

The most active chemotherapeutic compounds which are not phytotoxic are:
o-nitrosophenol.$NiCl_2$ complex, 1-nitroso-2-naphthol, p-nitrosophenol, o-nitroso-p-chlorophenol.$CuSO_4$ complex, p-nitrosodimethylaniline. H_3PO_4 salt, p-nitrosodimethylaniline.$ZnCl_2$ complex, p-nitrosodiphenylamine.$CuCl_2$ complex, nickel chloride, p-nitrosodimethyl-

aniline.$CoCl_2$ complex, p-nitrosophenol.$NiCl_2$ complex, o-nitrosophenol.$ZnSO_4$ complex, 1-nitroso-2-naphthol-3,6-disulphonic acid (sodium salt).$NiCl_2$ complex.

It was a disappointment that p-nitrosodimethylaniline proved to be too phytotoxic; even with a solution of this compound that just showed a slight chemotherapeutic activity the symptoms of its toxic effect appeared. Therefore it was investigated whether complexes formed by p-nitrosodimethylaniline and metal salts, such as $CoCl_2$, $Ni(ClO_4)_2$, $MnCl_2$, $CaCl_2$, $ZnCl_2$ and $CuCl_2$, would give better results. The experiments showed that the $CoCl_2$ and $Ni(ClO_4)_2$ complexes had a positive chemotherapeutic activity against TMV in *Nicotiana tabacum* (var. no. 11), while the $ZnCl_2$ complex suppressed TMV in *Nicotiana rustica*. No activity was observed with these compounds in a 0.1 % solution. However, the chemotherapeutic activity of these salts generally remained so far behind that of other nitroso compounds that these salts had to be excluded from further research.

It seemed worth while to determine whether these compounds were not toxic for rabbits either. It was demonstrated that comparatively large amounts (1–3 grams) of these compounds could daily be mixed with the food for 6 weeks without having any harmful effect on the animals. Examination of their organs (liver, spleen, kidney, etc.) did not reveal visible aberrations. These observations justified a more extensive investigation into the effect of these compounds.

3. INFLUENCE OF THIOURACIL AND THE NON-TOXIC CHEMOTHERAPEUTIC COMPOUNDS

First of all the influence of the non-toxic chemotherapeutic nitroso compounds on the incubation period of several viruses was determined (Table VII); this influence is expressed as the average of the percentage increase in the incubation period.

The normal incubation time strongly depends on the environmental and developmental conditions of the host plants. Moreover, the increase in incubation period due to treatment with a chemotherapeutic compound showed an approximately proportional variation rather than independence of the length of this period. As generally the results vary considerably from one occasion to another it was necessary to take the following precautions.

All the experiments had to be performed during the period from April to the end of August with young plants, in the four-leaf stage of development which had been grown under favourable conditions in a greenhouse and whose incubation time remained within the following lower and upper limits: 18 and 22 days for sugar beet, 8 and 10 days for tobacco and 10 and 12 days for beans and tomato, respectively.

In addition, the experiments with the most active compounds were repeated many times in the course of a period of 2 to 3 years. The calculation of the percentage increase of the incubation period approximately eliminates the small differences remaining between the incubation periods and renders the results better comparable.

TABLE VII

Influence of some non-phytotoxic nitroso compounds with chemotherapeutic activity

The compounds were applied according to the methods described in II. 6. The plants were infected with the virus 2 days after application of the chemical. S: spraying of a 0.1 % solution of the compound on the leaves; D: dipping of the roots in a 0.1 % solution of the compound for 24 hours; N: adding of 15 mg of the compound to 150 ml of Knopp's nutrient solution. I = 2-nitrosoisobutyric amide; II = o-nitroso-p-chlorophenol.$CuSO_4$ complex; III = p-nitrosophenol; IV = o-nitrosophenol.$NiCl_2$ complex; V = 1-nitroso-2-naphthol.

Virus	Host plant	Method of application	Average percentage increase in incubation period after adding				
			I	II	III	IV	V
Yellow virus	Sugar beet	S	0	10	4	6	8 ± 1.3
		D or N	0	8	10	12	10 ± 1.9
TMV	Nicotiana rustica	S	10	30	14	26	21 ± 4.4
		D or N	10	30	16	18	14 ± 4.1
	Nicotiana tabacum	S	16	6	10	40	8 ± 2.4
		D or N	14	14	22	38	19 ± 4.1
	Nicotiana glutinosa	S	0	10	4	6	(25 replicates)
		D or N	0	0	6	6	
Phaseolus virus 1	French bean	S	10	10	26	4	
		D or N	12	6	20	10	
Phaseolus virus 2	Broad bean	S	0	4	14	10	
		D or N	0	10	16	4	

Table VII confirms that α-nitrosoisobutyric amide has a moderate chemotherapeutic activity, whereas 1-nitroso-2-naphthol, o-nitroso-p-chlorophenol. $CuSO_4$ complex, p-nitrosophenol and o-nitrosophenol. $NiCl_2$ complex belong to the most active compounds tested.

The question may arise whether the effect of a chemotherapeutic compound depends on the type of virus, the host plant and the way this compound entered the plant. Now the individual observations show considerable variation and this prevents making a general inference. Table VII, however, enables the conclusion to be drawn that the activity of a chemotherapeutic substance may depend on the factors mentioned. It appeared that 2-nitrosoisobutyric amide in 0.1 % solution does not interfere with the development of yellow virus in sugar beet, of TMV in *Nicotiana glutinosa* or of Phaseolus virus 2 in broad bean; p-nitrosophenol strongly inhibits the development of the last-mentioned virus, whereas it hardly interferes with the propagation of TMV in *Nicotiana glutinosa.* In some cases the way in which the chemotherapeutic substance enters the plant is of great importance to its activity. However, it must be admitted that it is not easy to draw conclusions from our experiments, as the quantity of active compound penetrating into the cells is not known. Therefore, the differences in activity may be attributed to differences in permeability as well as to specific reactions of the viruses and host plants.

S = spraying of the leaves. < = concentration just phytotoxic.

Virus	Host plant	p-Nitrosophenol				1-Nitroso-2-naphthol (Na or K salt)				o-Nitroso-p-chlorophenol (copper complex)				Thiouracil				Mixture of thiouracil and p-nitroso-phenol or 1-nitroso-2-naphthol			
		A		B		A		B		A		B		A		B		A		B	
		D	S	D	S	D	S	D	S	D	S	D	S	D	S	D		D	S	D	S
		%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%				
TMV	Nicotiana rustica or Nicotiana tabacum	0.1	0.1	0.20	0.25	0.1	0.1	0.15	0.25	0.1	0.1	0.20	0.25	0.05 [1]	0.1 [1]	0.01 [1]	0.05	0.05/0.05 %	0.05/0.05 %	< 0.05/0.05 %	0.05/0.05 %
	Nicotiana glutinosa	0.1	0.1	0.20	0.25	0.1	0.1	0.15	0.2	0.1	0.1	0.20	0.25	0.05 [1]	0.1 [1]	0.01	0.05	0.05/0.05 %	0.05/0.05 %	< 0.05/0.05 %	0.05/0.05 %
	tomato	0.1	0.1	0.20	0.25	0.1	0.1	0.15	0·	0.1	0.1	0.20	2. 25	0.05 [1]	0.1 [1]	0.01	0.05	0.05/0.05 %	0.05/0.05 %	< 0.05/0.05 %	0.05/0.05 %
Phaseolus virus 1 or 2	French bean or broad bean	0.05	0.1	0.20	0.25	0.05	0.1	0.1	0.25					0.05 [1]	0.1 [1]	0.005	<0.1	0.05/0.05 %	0.05/0.05 %	< 0.05/0.05 %	< 0.05/0.05 %
yellow virus	sugar beet	0.1	0.1	0.20	0.25	0.1	0.1	0.25	0.25	0.1	0.1	0.20	0.25	0.05 [1]	0.1 [1]	0.01	0.05				

[1] In experiments with toxic compounds it is often difficult to note the minimum concentrations with a chemotherapeutic effect.

It seemed desirable to investigate for the most active chemotherapeutic compounds whether there is a large difference between the minimum concentration bringing about an anti-virus effect and the maximum concentration that does not cause any symptoms of damage to the host plants. Table VIII gives the results of one of these experiments; thiouracil was included as a phytotoxic substance. The lowest concentration of this compound that still counteracted the virus always had a marked injurious effect on the host plants, whereas with p-nitrosophenol and the copper complex of o-nitroso-p-chlorophenol there was a definite difference between the critical concentrations: the toxic effect appeared at a concentration 2-2.5 times as high as the one leading to a chemotherapeutic effect.

Solutions containing both thiouracil and p-nitrosophenol or thiouracil and 1-nitroso-2-naphthol were also tested. It might be expected that with these solutions, considering the much lower concentration of thiouracil, the chemotherapeutic effect of this compound would be relatively more pronounced than its injurious effect. This was definitely the case, but the effect was insufficient, the mixtures still being too toxic, particularly for French and broad beans.

IV. FIELD EXPERIMENTS

1. Introduction

The experiments described in the preceding chapter were carried out with seedlings a few weeks old. It may be expected, however, that the response of such young plants, grown in a greenhouse and artificially infected with virus, to a treatment with chemotherapeutic compounds will differ considerably from that of older or full-grown plants in the field which have been infected with virus under natural conditions. The compounds may have a stronger effect on seedlings than on full-grown plants; moreover, the consequences of a virus infection may be more harmful to young plants, when they are insufficiently protected by the chemotherapeutic agents. On the other hand, in field experiments these compounds have to remain active for some considerable time, as infection may occur on several occasions; this prolonged activity can be obtained by more frequent application of the chemical. For these reasons it seemed appropriate to perform several series of field experiments in the course of five years.

The response to chemotherapeutic treatment was determined by comparing the yields of virus-infected plants in treated and in untreated field plots. It is obvious that only those compounds were chosen which in the experiments described in Chapter III had produced the best results.

In 1953, the first year of our field experiments, 0.1 % solutions of p-nitroso-phenol, the potassium salt of 1-nitroso-2-naphthol and of thiouracil, as well as 50/50 mixtures of thiouracil and one of the nitroso solutions mentioned were sprayed in high volume (1000 litres/hectare), once or twice before and once, twice or three times after inoculation at intervals of about two weeks. The chemotherapeutic activity was tested on Phaseolus virus 2 in broad beans, Phaseolus virus 1 in French beans, and on TMV in *Nicotiana tabacum* (var. no 11 and White Burley) and *Nicotiana rustica.*

The first results obtained were so promising that in the following years the investigation was continued with more extensive field experiments. Thiouracil and its mixtures were not further examined on account of their phytotoxicity to the bean plants, which resulted in a considerable decrease in seed production. Experiments on the effect of 1-nitroso-2-naphthol-3,6-disulphonic acid (Na salt), o-nitrosophenol.$NiCl_2$ complex and o-nitroso-p-chlorophenol.$CuSO_4$ complex were now included.

The effect of all the compounds sprayed on virus development was investigated by varying the concentration range from 0.05 % to 2.0 %, by repeating the spraying 3–8 times or by varying the spraying period (before, at the time of or after natural infection by aphids).

The investigations were extended to comprise yellow virus and sugar beet; in fact, with these plants by far the most trials were performed.

A few experiments were done in which the above-mentioned compounds were used as seed dressings. The experimental conditions remained otherwise unchanged.

The field plots were situated in different regions of the Netherlands: in the experimental garden of the Koninklijke/Shell Laboratory at Amsterdam; in the Eemnesserpolder1); at Renkum; at Well, Bergen and Siebengewald in the Northern part of Limburg—one of the areas where virus yellows causes most serious damage to the sugar beet

TABLE IX

Climatological conditions during the years of the field experiments

Deviations from the average temperature (° C) and average rainfall (in millimetres) in the Netherlands (de Bilt) from 1953–1958. The standard values used are those calculated for 1955 over the period 1921–1950.

Season	Average temp., ° C	Deviation (° C) from average in				
		1953	1954	1955	1957	1958
March–May	8.6	+ 0.3	— 0.1	— 2.0	+ 0.5	— 1.6
June–August	16.4	+ 0.1	— 1.4	+ 0.3	+ 0.4	— 0.2
September–November	9.8	+ 1.3	+ 0.9	+ 0.3	— 0.2	+ 0.9

Season	Average rainfall, mm	Deviation (%) from average in				
		1953	1954	1955	1957	1958
March–May	150	— 34	— 14	0	— 10	— 6
June–August	214	+ 38	+ 52	— 35	+ 35	+ 7
September–November	218	— 69	+ 20	— 5	+ 25	— 16

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1) The author is very much endebted to the management of the "Koninklijke Beetwortelzaad Cultuur Kuhn and Co", Naarden for the use of a part of their experimental field, and for the harvest analysis, free of charge, performed by them in 1953.

crop—and in the experimental garden of I.P.O. at Wageningen.

In the following sections the experiments carried out to limit the effect of the virus infections mentioned and their results are described. A survey of the climatological conditions during the years these experiments were done is given in Table IX.

2. Bean viruses in broad bean and French bean

In 1953 and 1954 the effect of p-nitrosophenol, of 1-nitroso-2-naphthol (K-salt) and of o-nitroso-phenol ($NiCl_2$ complex) was determined, in small experiments; the 1954 results on broad bean are recorded in Table X.

TABLE X

Preliminary experiments on the effect of chemotherapeutic compounds on the yield of broad bean plants inoculated with Phaseolus virus 2

Two experiments, 20 plants per plot of 2½ square metres. Exp. A: Seedlings planted on 12-4-1954; Sprayed on 14-5, 19-5, 3-6 and 17-6-1954; Inoculated by hand on 21-5-1954. Exp. B: Seeds sown on 12-4-1954. Sprayed on 3-3, 14-6, 17-6 and 24-6-1954; Inoculated by hand on 21-6-1954. Natural infection by aphids also occurred; insects killed with a parathion spray (0.05 %) on 11-6-1954. Harvest on 22-7-1954. Yield on infected untreated plants: Exp. A: 100 seed pods, weight 810 g; Exp. B: 235 seed pods, weight 2540 g.

Spraying compound	Experiment	Concentration of spraying solution			
		0.1 %		0.2 %	
		% increase of yield as compared with infected untreated plants			
		nr. of pods	weight	nr. of pods	weight
p-nitrosophenol	A	+ 130	+ 160	+ 70	+ 140
	B	+ 20	+ 40	— 30	— 20
1-nitroso-2-naphthol (K salt)	A	— 10	+ 20	+ 80	+ 100
	B	0	— 10	+ 20	+ 20
1-nitroso-2-naphthol-3,6-disulphonic acid (Na salt)	A	+ 30	+ 50	+ 80	+ 110
	B	0	0	+ 20	+ 30
o-nitrosophenol ($NiCl_2$ complex)	A	+ 10	+ 90		
	B	0	+ 10		

These experiments were only of a tentative nature, the number of replicates was too small. The same applies to the experiments in which the effect of these chemicals on French bean was determined.

All these results go to show that p-nitrosophenol may have chemotherapeutic activity in comparatively low concentrations (0.1 %). The nitrosonaphthols had a favourable effect rather at higher concentrations (0.2 %), although when applied on French bean these compounds were also active at 0.1 %. It will be seen that the figures of Table X show a considerable variation. This is also due to the fact that a small favourable effect of spraying will result in a relatively high percentage increase when the plants are heavily attacked by the virus, whereas this value is relatively low when the virus disease does not seriously affect the plants.

3. YELLOW VIRUS IN SUGAR BEET PLANTS

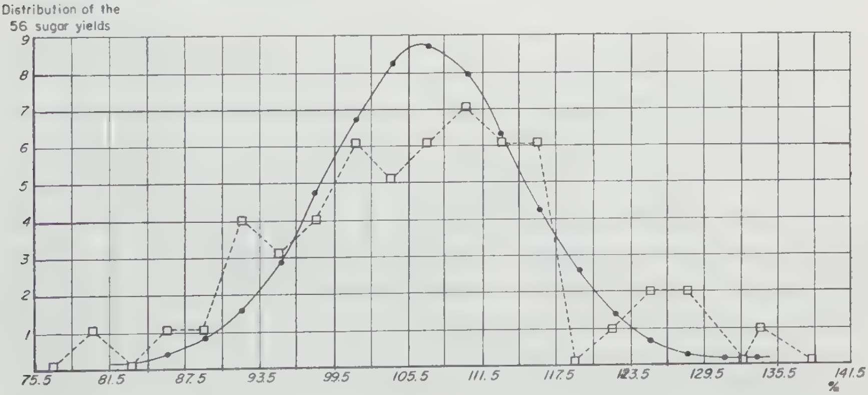
In the period of 1954–1958 experiments were undertaken in order to establish the influence of spraying sugar beet infected with yellow virus with nitroso compounds. This was done by determining the sugar yield of sprayed and unsprayed plots of sugar beet.

The seeds were drilled in rows of 35 or 40 centimetres and singled out at distances of 20–32 centimetres to obtain the same density as in a field with 70,000 plants/hectare.

It has often been suggested (LÜDECKE 1945, SCHOENE 1954, SIMON 1954) to grow sugar beet crops at a higher density, even up to 100.000 plants/hectare. The area is sooner covered by the crop and this is attractive. For the aphids prefer a crop with open spots, which often occur in fields containing 50–60.000 beet plants/hectare. At this density, however, the root crop develops better.

It is worth mentioning that the trial plots in the northern part of Limburg were situated in a field of a few hectares on which sugar beets were grown. The plants were infected with yellow virus in the natural way by aphids. In 1954 the aphids appeared rather late due to the cold weather. Hence the first symptoms of the disease did not appear until 10th July, about a fortnight later than in normal years.

In the other experiments, viz. those at Amsterdam, in the Eemnesserpolder, at Renkum and in the I.P.O. garden in Wageningen, the plants were cultivated in experimental fields. They were infected by placing 6–10 aphids on every plant, as it was not quite certain that the natural infection would be sufficient. A few days later the aphids were killed by a Systox spray in order to prevent the aphids from migrating to other crops in the neighbourhood. The symptoms of the disease became visible at the expected time, about three weeks after the date of infection.



Graph. 1 Frequency distribution of yield of sugar beet plants infected with sugar beet yellow virus and sprayed with $0.1^0/_0$ solution of 1-nitroso-2-naphtol (potassium salt)

Yield of sprayed plants expressed in $^0/_0$ of yield of untreated control plants

•——• normal distribution curve

□- - - -□ experimental distribution curve

All experiments were performed in blocks with plots of 14 or 28 square metres (100–200 beet plants). These plots were randomized to enable a variance analysis to be made at harvest time according to the Fischer (1951)—Kuiper (1952) methods. Invariably 3–5 replicates were investigated at the same place and time and the average value of the analysis was regarded as its results.

In all, 56 field experiments in which sugar beet plants were sprayed with 1-nitroso-2-naphthol in 0.1 % solution were carried out in 5 years. The sugar yield of 100 virus-infected plants treated with this compound was 107 % ± 1.5 of the yield of the infected but untreated control plants. The increase, though small, was significant. Graph 1 shows the frequency distribution curve of the sugar yield together with the normal theoretical frequency distribution curve best fitting it. The two curves show a fair agreement.

Treating the sugar beet plants with more dilute solutions gave less favourable results: spraying with 0.05 % solutions also increased the sugar yield, but this effect was less marked than that obtained with 0.1 % solutions. Treating the plants with solutions of 0.2 % or higher gave decidedly poor results; phytotoxic phenomena were observed, which often neutralized the expected chemotherapeutic effect. That is the reason why, considering all the field experiments (68 in all) in which 1-nitroso-2-naphthol was sprayed in a concentration range of 0.05–0.2 %, the average increase in sugar yield of 100 plants was only 5 % ± 1.5. From these experiments it can be concluded that the minimum concentration limits having a positive chemotherapeutic and an injurious effect do not differ much. It is not altogether precluded that the two phenomena spring from a common source, the more so because strong indications were obtained that more than 3 sprayings with 0.1 % also resulted in a phytotoxic effect competitive to the chemotherapeutic activity.

The field experiments with the other compounds tested were less extensive. Spraying with the copper sulphate complex of o-nitroso-p-chlorophenol produced an increase in sugar yield of 100 plants of 11 % ± 4. Although this figure is not fully reliable, it may be expected that if considerably more experiments are carried out than the number of 10 now performed this compound will prove to have a small positive chemotherapeutic effect. The other compounds tested did not bring about a significant increase of the yield: with p-nitrosophenol 2 % ± 4 and with 1-nitroso-2-napthol-3,6-disulphonic acid (Na salt) 6 % ± 5.

4. Yellow virus in sugar beet stecklings

A few small experiments were performed to investigate whether the seed production of diseased stecklings can be increased by dipping them for 18½ hours in a 0.05 % solution of nitroso compounds before they are planted out in spring. Nine stecklings, to be used as controls, were dipped in water for 18½ hours.

By this procedure the solution penetrates 1–2 centimetres into the root tissues, the root showing the brownish-yellow colour of the nitroso compounds over this distance. During the growing period of the stecklings they are sprayed 3 times with a 0.1 % solution of the compound tested in order to reduce the effect of secondary infections.

The stecklings were never cured by dipping, but already during growth it appeared that the untreated control plants were more severely attacked than the treated ones. These differences became very pronounced at harvest time: the treated plants produced more seeds (Table XI). The potassium salt of 1-nitroso-2-naphthol had stimulated the seed production of the infected seedlings considerably, although it did not exceed 45 % of that of normal uninfected plants.

TABLE XI

Seed production of infected sugar beet stecklings after treatment with various nitroso compounds

Stecklings dipped in 0.05 % solutions of nitroso compounds for 18½ hours. Control stecklings dipped in water. Stecklings planted after one day (3-5-1955). Spraying on 9-6, 1-7 and 15-7-1955 with 0.1 % solution (1000 litres/hectare). Harvest: 22-9-1955. Seed production of uninfected plants: about 240 g/plant.

	Number of stecklings	Yield of seeds, g/plant
Untreated stecklings	9	50
Stecklings treated with:		
p-nitrosophenol	9	67
1-nitroso-2-naphthol (K salt)	8	108
o-nitroso-p-chlorophenol ($CuSO_4$ complex)	9	57

Probably the increase in yield after treatment with p-nitrosophenol, although less marked, is also significant.

These results can only be obtained when the lethal effect of the virus infection does not exceed certain limits; when the plants are severely attacked no favourable effect of the nitroso compounds can be observed or expected. Table XII gives the results of an experiment in which the virus infection was particularly harmful; the seed production of infected plants was about 1/10 of that of normal healthy plants.

TABLE XII

Seed production of sugar beet stecklings severely attacked by virus yellows after treatment with various nitroso compounds

Samples of 54–79 heavily infected sugar beet stecklings were planted out in the field about mid-April 1956. The experimental plants were watered (50 ml, 0.1 % solution per plant) on 27-4-1956. To prevent secondary infection these plants were sprayed on 22-6 and 9-7 (0.1 % solution; 1000 litres/hectare). Harvest on 9-10-56. Normal healthy stecklings produce about 240 g seeds/plant.

	Number of stecklings	Yield of seeds, g/plant
Untreated stecklings	79	25
Stecklings treated with:		
p-nitrosophenol	54	26
1-nitroso-2-naphthol (K salt)	55	26

5. TMV IN TOBACCO

In several series of experiments TMV-infected tobacco plants (*Nicotiana rustica*, *Nicotiana tabacum* var. no. 11; *Nicotiana tabacum* var. White Burley) were sprayed in 0.1 or 0.2 % concentrations with solutions of p-nitrosophenol or the potassium salt of 1-nitroso-2-naphthol.

Slight indications of a chemotherapeutic effect of both compounds were obtained; especially the results with the potassium salt of 1-nitroso-2-naphthol in 0.2 % solution against TMV in *Nicotiana rustica* were rather convincing.

The experiments with *Nicotiana tabacum* var. White Burley were not so successful, as the plants grew slowly and consequently the propagation of the virus was not very fast.

Experiments with thiouracil alone were not carried out on account of the phytotoxicity it had shown in greenhouse experiments. Instead, thiouracil mixed with a nitroso compound was used.

Positive results were obtained with TMV-infected plants of *Nicotiana tabacum* var. no. 11 sprayed with solutions containing thiouracil (0.05 %) and p-nitrosophenol (0.05 %) or 1-nitroso-2-naphthol (0.05 %). Table XIII lists the results of an experiment in which the influence of spraying on the incubation time was determined in relation to the growth season.

TABLE XIII

Increase of the incubation time by spraying Nicotiana tabacum var. no. 11 with solutions containing thiouracil and a nitroso compound

Each exp. comprised 12 plants of Nicotiana tabacum var. no. 11. The plants were sown in various months and had a length of about 30 cm at the beginning of the exp. In the first and second exp. the plants were sprayed 6 times, with intervals of 3 days. Inoculation with TMV after the third spraying. In the third, fourth and fifth exp. the plants were sprayed 2–3 times, with intervals of 3–7 days. Inoculation with TMV after the first spraying. Spraying solution: thiouracil (0.05 %) and a nitroso compound (0.05 %).

Period during which the experiment was carried out	Incubation time of unsprayed plants, days	Incubation time (days) of plants sprayed with	
		p-nitrosophenol + thiouracil	1-nitroso-2-naphthol + thiouracil
April–May	25 ± 0.5	—	30 ± 1.1
May–June	14 ± 0.5	34 ± 1.5	—
July–August	11 ± 0.5	25 ± 1.–	25 ± 1.–
August–September	22 ± 1.–	31 ± 2.–	31 ± 1.5
September–October	28 ± 1.5	37 ± 0.8	37 ± 0.8

The plants grew very well when sown early (spring, early summer), but the growth rate decreased considerably when sown later (mid-summer, autumn). The experiment started when the plants had a height of about 30 cm. The incubation time of TMV-infected plants decreased for those sown during the period of April to July, but increased considerably in the case of those sown later on; without doubt this was due to environmental conditions, particularly as regards light and temperature. Spraying of the plants with the solutions already mentioned resulted in a marked increase in incubation time; the seasonal decrease of the incubation time displayed by the unsprayed plants disappeared almost entirely. Therefore, spraying was most effective in the period of May till August. As a consequence of the inhibitory effect of these compounds on the development of TMV, the visible symptoms were less pronounced in all the experiments.

The influence of spraying with these solutions was also investigated on *Nicotiana rustica* (Table XIV).

TABLE XIV

Influence of spraying with solutions containing thiouracil and a nitroso compound on the development of TMV-infected Nicotiana rustica plants

Each exp. comprised 12 plants of Nicotiana rustica. The plants had a length of about 30 cm at the beginning of the exp. Spraying 3 times (9, 21 and 24-7-1953) with a spraying solution containing thiouracil (0.05 %) and a nitroso compound (0.05 %). Control plants sprayed with water. Plants inoculated with TMV on 16-7-1953.

Sprayed with	Percentage of diseased plants				Length of plants on 12-8-1953, cm	Number of leaves larger than 20 by 25 cm on 1-9-1953	
	31-7	3-8	10-8	17-8		no visible TMV symptoms	with TMV symptoms
A. *Non-infected plants*							
water	0	0	0	0	85 ± 2.6 (flowers)	11 ± 0.2	
p-nitrosophenol + thiouracil	0	0	0	0	83 ± 3.– (a few fl.)	11 ± 0.3	
1-nitroso-2-naphthol + thiouracil	0	0	0	0	79 ± 1.8 (no flowers)	11 ± 0.6	
B. *TMV-infected plants*							
water	100	100	100	100	57 ± 2.6	4 ± 0.4	4 ± 0.3
p-nitrosophenol + thiouracil	0	25	83	92	68 ± 2.1	7 ± 0.3	2 ± 0.4
1-nitroso-2-naphthol + thiouracil	0	33	75	92	68 ± 3.3	8 ± 0.5	2 ± 0.6

Here, too, spraying did not prevent the outbreak of the disease, but it reduced its rate of development considerably. Consequently, the plants grew better than the control ones. There was a marked increase in the number of full-grown leaves, which seem to be of some inportance with regard to the industrial use of tobacco leaves. This can easily be explained. TMV causes top necrosis and dying off of the growing point. As, according to the preceding experiment, spraying delays the outbreak of the disease the plant reaches a later stage of development in the meantime. The total number of leaves increases somewhat and the number of leaves with visible symptoms decreases. Therefore, the consequences of the infection are less serious.

Surprisingly enough, these solutions, although they contained thiouracil (if only 0.05 %), had no appreciable injurious effect on the tobacco varieties tested. It should be borne in mind, however, that in these experiments it is the production of ful-grown leaves that counts, whereas in the bean experiments the seed production was determined.

V. GENERAL DISCUSSION

1. Introduction

In the experiments described in Chapters III and IV the performance of several nitroso compounds and of thiouracil in reducing the harmful and growth-inhibiting effect of several virus infections was investigated. It appeared that 1-nitroso-2-naphthol had a positive, though not very considerable chemotherapeutic effect on the plants tested: sugar beet infected with yellow virus, bean species with the bean viruses. Other nitroso compounds (p-nitrosophenol, 1-nitroso-2-naphthol-3,6-disulphonic acid (Na salt) and the copper sulphate complex of o-nitroso-p-chlorophenol) also proved to have a favourable effect. Thiouracil was too toxic to be of any value. It could be demonstrated, however, that solutions containing thiouracil and p-nitrosophenol, in which the concentration of each of these substances was so low (0.05 %) as to have only a slight influence on the development of the virus, brought about a considerable increase in incubation period and growth of *Nicotiana rustica* and *Nicotiana tabacum* var. no. 11 plants infected with TMV. In addition, these solutions were not noticeably harmful to these plants.

Unfortunately, field experiments on a scale large enough to warrant significant results have only been carried out with sugar beet plants infected with yellow virus and sprayed with 1-nitroso-2-naphthol (K salt). These experiments showed a small, but positive chemotherapeutic effect of the compound. Small-scale field experiments on TMV-infected tobacco species with solutions of thiouracil and a nitroso compound also resulted in a significant positive effect.

It could be demonstrated that 1-nitroso-2-naphthol and p-nitrosophenol have no perceptible influence on the virus in vitro. Equal volumes of 0.2 % TMV and of 0.2 % of one of the nitroso compounds investigated were mixed and kept at room temperature (18° C) for different times, varying from 2–24 hours. At the end of these periods five tobacco plants were inoculated with the mixture in the ordinary way. Control plants were treated in the same way with a TMV solution of the same concentration, without a nitroso compound being added. No differences in incubation time and severity of attack by the disease were found between the plants inoculated with these mixtures and the control plants. It would have been better if the tests had been done with a series of dilutions of the mixtures, because only with the smallest amount of virus capable of producing infection one can really prove that the nitroso compounds have no influence on the virus in vitro. Nevertheless these experiments gave strong indications that the virus is not inactivated, the more so as it must be expected that the concentration of these nitroso compounds in the plant cells is much less than in the solutions tested. Moreover, electron microscopic examination of the virus particles with the aid of the shadow casting technique with Pd did not substantiate the assumption of a reaction in vitro: virus particles remaining in the nitroso solutions did not differ in any respect from those of the untreated virus, a particular point being that the virus particles were not disintegrated.

2. Effect of nitroso compounds on the virus alone

The experiments described in Section V.1 have shown that 1-nitroso-2-naphthol and p-nitrosophenol have no perceptible influence on the virus in vitro. It must be assumed, therefore, that the compounds tested act inside the plant cells. Here they can either inhibit the virus production or stimulate the plant to destroy the virus particles by producing "antigenic substances". The latter hypothesis was not investigated as it would have required extracting these antigenic substances and testing them for antivirus activity.

The virus propagation is different according as the nitroso compounds are applied to the plant before, simultaneously with or after the virus infection. Application of the chemotherapeutic compounds several days before the incubation date has no effect; the compound has already been inactivated. Therefore the application of the chemotherapeutic compound was standardized: in all the experiments the plants were sprayed 2 days before infection. During this time the chemical has ample opportunity to penetrate into the plant.

Spraying three or more days after infection with p-nitrosophenol or with 1-nitroso-2-naphthol was, in most cases, ineffective. With *Nicotiana rustica* and often with White Burley, spraying one or two days after inoculation still produced a chemotherapeutic effect. These results suggest that the incubation time of TMV in *Nicotiana rustica* only increases under the influence of the antivirus factor, when the virus propagation has not yet reached its optimum rate and the translocation of the virus from the inoculated leaf towards the top has only just started.

No anti-virus effect can be expected when the concentration of the spraying solution is too low. On sugar beet plants 0.1 % solutions of p-nitrosophenol or 1-nitroso-2-naphthol had a marked inhibiting effect on the virus multiplication; plants sprayed with 0.05 % solutions gave a lower yield than those treated with 0.1 % solutions. These results could be confirmed serologically with 1-nitroso-2-naphthol treated plants. Therefore, as a rule 0.1 % was used, the more so as concentrations exceeding 0.1 % often led to phytotoxicity in field experiments. From the experiments described on page 394 and recorded in Table VIII it can be derived that for these compounds the highest permissible concentration at which no phytotoxicity occurs is nearly 0.2–0.25 %. Here a difference in behaviour between plants grown in the greenhouse and in the field manifests itself. Serological tests demonstrated a reduction in virus content of greenhouse and field plants treated with 0.15 and 0.2 % solutions. This reduction proved to be at least similar to that obtained with a 0.1 % solution.

Application of too much of the chemical by spraying too frequently (6–8 times) is often harmful; it was not found to decrease the virus content perceptibly.

During the incubation time the rate of virus production in White Burley tobacco plants treated with 1-nitroso-2-naphthol drops considerably. It was determined serologically that this compound may reduce the virus content to $^1/_2$–$^1/_{64}$ of the amount in treated control plants. Complete destruction of the virus hardly ever occurred, so that the visible symptoms of the disease still appeared, though the incubation time had increased, sometimes by as much as 10 days. But even when these symptoms are perceptible the virus content is still lower than in the untreated plants. A similar effect can be expected on *Nicotiana rustica* and sugar beet.

It is a well-known fact that few virus particles suffice to infect a plant systemically. However, infecting with a small number of virus particles cannot be done, because only few virus particles of an inoculum "strike", as is known from the experiments with the local lesion method on *Nicotiana glutinosa*. Therefore, in the greenhouse experiments and in the field experiments with artificial infection the quantities of infecting material used were on the safe side to warrant infection (see II.4), thus always a hundred to a thousand times larger than the required minimum. The practice to use the appearance of the first visible symptoms as a yardstick for anti-virus activity is, therefore, not quite reliable. It may be expected that often many virus particles are destroyed by a chemical, but the few that remain will cause the plant to become diseased all the same.

Some field experiments were performed with diseased sugar beet stecklings. Satisfactory results were obtained with 1-nitroso-2-naphthol (K salt) and with p-nitrosophenol when the plants were only mildly infected. Severely attacked stecklings, however, did not respond to treatment with these compounds (see Tables XI and XII).

Another condition that must be fulfilled for a positive effect to be obtained is that the plants are young and growing at optimum rate. In spring the increase in incubation time due to treatment with nitroso derivatives is greater than in late summer and in autumn under otherwise similar conditions (see Table XIII). This must be attributed to the plants growing under sub-optimum conditions in the latter case. A similar effect is observed with sugar beet and the two bean species.

The climatological conditions also have some, though usually only little, influence; the differences observed are to be regarded as secondary consequences of the changing growth rates of the plants.

The results of spraying with chemotherapeutic compounds were derived from yield analyses, from observations on the moment of appearance and the development of the visible symptoms of the disease, and from serological determinations of the virus content of the plants. The last two methods are direct ones. In addition, the influence of the compounds on virus development was also traced with the aid of the following indirect methods for determining the virus activity: the reducing sugar test, the reso blue test, the 2, 3, 5-triphenyl tetrazolium chloride (TTC) test and the respiration test. The variability of all these tests, however, proved to be so great that no reliable results could be obtained. These tests, particularly the reducing sugar test, did demonstrate the presence of virus in the infected plants, often during the incubation period already, but on account of the large spread in results the improvement caused by treatment with 1-nitroso-2-naphthol could not be proved significantly. The TTC, the reso blue and the respiration test were so insensitive that during the incubation time not even differences between healthy and infected plants could be demonstrated significantly. Under these circumstances it was of no avail to use these methods to investigate the effect of the nitroso compounds on the test plants.

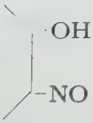
3. Stability of the chemical in the plant

It is important to investigate whether the nitroso compounds remain unchanged in the plant tissues or whether they are decomposed. Therefore microchemical tests were performed with treated tobacco, sugar beet and even tulip plants. They have been borrowed from Feigl (1956); four of them proved to give reliable results.

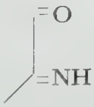
Briefly, the procedure of these tests, performed with chemical but without plants, is as follows:

(a) A few milligrams of the powdered 1-nitroso-2-naphthol is melted in a microcrucible along with some milligrams of phenol. After cooling, a drop of concentrated sulphuric acid is added. The liquid turns dark chery-red. After diluting with water, the solution is made alkaline with a few drops of 4 N sodium hydroxide. It then turns deep blue (Liebermann test). By means of this test 0.4 μ grams of p-nitrosophenol or 0.5 μ grams of 1-nitroso-2-naphthol can be identified. Generally aliphatic nitroso and iso-nitroso compounds and aromatic nitroso compounds give this reaction. The sulphuric acid probably saponifies the nitroso compounds; the nitrous acid produced nitrosates the phenol in the unoccupied p-position.

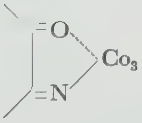
(b) A drop of 0.1 % cobalt nitrate solution is added to about 0.1–1.0 ml of 0.1 % 1-nitroso-2-naphthol. A positive response is signalled by a brown-red colour, which is resistant to 2 N sulphuric acid. In this reaction the o-nitrosophenols (I) are in equilibrium with their tautomeric o-quinone oxime forms (II), which combine with trivalent cobalt ions containing this metal in the chelate ring (III):



I



II

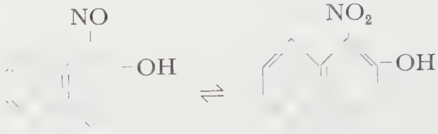


III

The test reveals 1 μ gram of 1-nitroso-2-naphthol and 5 μ grams of 1-nitroso-2-naphthol-3,6-disulphonic acid (Na salt).

(c) A quantity of 0.1–1.0 ml of 0.1 % 1-nitroso-2-naphthol is mixed in a test tube with a drop of an aqueous tyrosine solution of about 100 ppm and heated.

A drop of concentrated nitric acid is added to the hot solution. A bright purple colour appears which gradually fades. The chemistry of this reaction is unknown. An essential step seems to be that the nitric acid apparently oxidizes the 1-nitroso-2-naphthol (I) to 1-nitro-2-naphthol (II), and this reaction product reacts with tyrosine.



I II

Limit of identification: 0.5–1.0 μ grams of 1-nitroso-2-naphthol. This test was described by Feigl as a tyrosine test.

(d) A drop of 1-nitroso-2-naphthol (0.1 %) or a few milligrams of this chemical is mixed with 1 or 2 millilitres of a freshly prepared 1 % solution of sodium pentacyanoammine ferroate (prussic salt). After about 5 minutes an intense green colour is formed. With sodium pentacyanoaquo ferroate the same reaction takes place. This colour reaction depends on the exchange of the water or ammonia molecule of the prussic salt for a molecule of the nitroso compound:

$$Na_3[Fe(Cn)_5NH_3] + RNO \rightarrow NH_3 + Na_3[Fe(CN)_5RNO]$$
$$Na_3[Fe(CN)_5H_2O] + RNO \rightarrow H_2O + Na_3[Fe(CN)_5RNO]$$

It is noteworthy that the entrance of the RNO molecule into the inner sphere of the prussic salt, with expulsion of the NH_3 or H_2O molecule, occurs only in the light; it is a photoreaction. Limits of identification: 1 μ gram for 1-nitroso-2-naphthol and 0.15 μ grams for p-nitrosophenol.

These four tests, especially reactions (b) and (c) gave in vitro, good response. They could equally well be applied when the compounds were added to ground plant material immediately before the determination. Ground plant material in 1-nitroso-2-naphthol gave a weaker reaction than the corresponding control solution. Any substances interfering with the determinations were practically absent in the plant.

In plants sprayed with a 0.1 % solution of 1-nitroso-2-naphthol in the usual way (50 mg/½ sq. metre) a long time or just before they were examined by one of these tests, not a trace of this chemical could be detected; thus, less than 1μ gram was available in the solution of the tested plant material. As ½ square metre is just covered by 18 plants, which should receive all 50 mg of the compound dissolved in 50 ml water containing acetone and wetting agent, one plant will have absorbed 3 mg = 3000 μ grams. It can hardly be imagined that 3000 times the amount of 1 μ gram is lost because it did not reach the plants or did not penetrate into them.

Since it is difficult to determine how much of the spraying substance is received by a plant, the dipping method was used in the further experiments. The volume of solution taken up by the plants is easier to determine. The plants to be tested were dipped with their roots or stems in a solution of 1-nitroso-2-naphthol (0.1–0.2 % w) for varying times (1-5 days). During this period relatively large amounts of the compound were absorbed: in 5 days about 5 ml or 5000 μ grams of its solution per plant. The stem, also the large veins and even the smaller ones in the leaves were coloured dark brown. At the end of the experiment always one plant was rinsed with water and ground, the pulp being extracted with water or acetone. The total volume of the extracts was about 50 ml, which was tested. For each determination according to one of the four microchemical reactions 2–10 ml of the extracts were used. The reaction was invariably negative, like the reaction on the pulp residue. Thus, no nitroso compound could be detected. This proves that less than 1/5000 of the amount of chemical that has been absorbed remains as such in the plant.

Negative results were also obtained when after dipping the plant material was dried first or deep-frozen at the end of the experiment, or when the water or acetone extract was evaporated, preferably in vacuo, to a very small volume. These results can only be explained by assuming a rapid decomposition of the substance in the plant tissue.

The distribution of the brown colouring substance found in the stems and veins of the leaves was investigated microscopically. This substance could be followed over a great distance in the smaller veins. In the vessels the brown colour was darker than that of the nitroso compounds used. This substance was found exclusively in the xylem, expecially in the ring- and net vessels. It could not be established whether the phloem parts of the stele also contained this substance; the perecambium and the parenchym cells of the roots were free from it. It was important to determine whether the chemical reaches the cells of the inoculated leaves. The presence of the nitroso substance or its decomposition products in the leaf cells could not be demonstrated, either microscopically or microchemically.

It must thus be assumed that 1-nitroso-2-naphthol or its decomposition products exert an extremely strong inhibiting influence on the virus production, as the amount in the leaf cells must be very small. The second possible assumption, viz. that these compounds block the transport of the virus through the phloem, seems highly improbable, as in this tissue none of these substances could be detected.

4. Concluding remarks

These nitroso compounds, especially 1-nitroso-2-naphthol, greatly reduce the harmful effect of the virus infection.

Yet it is not fully established that they are antivirus factors, as it could not be demonstrated that they inactivate the virus either by chemical reaction or by interacting with the plant cell system producing the virus particle. As to thiouracil, it is often assumed that this compound interferes with the virus production through substituting the uracil. The effect of the nitroso-thiouracil mixtures as described on pp. 400 and 401 (Tables XIII and XIV) can be explained in the same way.

The activity of the nitroso compounds, however, is no less specific than that of thiouracil. An attractive supposition is that they act in a similar fashion and to speculate that a nitroso compound could react with uracil, or any other indispensable virus component available in the plant cells, forming e.g. a nitroso-uracil compound. In this way either inactive virus particles containing these nitroso compounds instead of the indispensable components might be formed or the virus synthesis would be inhibited. As soon as the nitroso compound is entirely decomposed the uracil (or the other indispensable virus component) formed in the plant again becomes available for virus synthesis and the plant is attacked by the disease after all; only the incubation time has increased considerably. If this hypothesis should be true the nitroso compound would act as an antivirus factor. On the other hand, such a hypothesis would also explain the fact that the phytotoxic and antivirus activities of these compounds are almost the same, as the plant itself needs uracil as well.

Further investigations into the problem of antivirus factors would be desirable. To be of practical use the antivirus activity of such substances should be higher and they would have to be more specific than the nitroso compounds tested in this investigation.

SUMMARY

(1) The object of the search described in this publication was to find "inhibitors of virus increase", not "inhibitors of infection".

(2) The investigations were performed with the following plants and viruses: tobacco species with tobacco mosaic virus (TMV); the disease causes leaf damage; sugar beet with virus yellows; the disease decreases root production; French bean and broad bean with Phaseolus viruses 1 and 2; the disease reduces seed production.

The cultivation method, the age of the plants tested, the virus, its purification and properties, and the techniques applied to infect the plants are briefly described.

The virus influence was investigated by means of direct methods, such as serology, and indirect ones, such as a reducing sugar test according to VAN DUUREN (1955), a reso blue test, (MÜNSTER (1955), SCHUSTER (1956)), to determine the callus production in the phloem (these two for sugar beet only), and a test with 2,3,5-triphenyl tetrazolium chloride (TTC) (see F. E. SMITH, 1951, and BEAL *et al.*, 1955). All the indirect tests, as well as the various tests with Nicotiana glutinosa, proved to be of little value (Tables II, III and IV).

(3) The chemicals were applied via the leaves (spraying, preferably as a 0.1 % solution, at a rate of 100 ml per square metre) or via the roots (dipping in a 0.1 % solution, or nutrient technique, 0.001–0.01 %w added to 150–200 ml Knopp's solution).

Table V lists the chemicals with antivirus properties described in the literature. Some of the most important are discussed separately (thiouracil, 8-azaguanine, malachite green, growth regulators and inorganic salts). On the basis of these data several types of chemicals were investigated. The nitroso hydroxyaryl compounds displayed such an activity that closer examination was justified.

The antivirus activity of a chemical was expressed as the percentage increase in incubation time; for this purpose the exact moment at which the first visible symptoms of the disease appear must be determined.

p-Nitrosophenol, 1-nitroso-2-naphthol, and the copper sulphate complex of o-nitroso-p-chlorophenol proved very attractive, being not too phytotoxic (Tables VI, VII and VIII); the potassium salt of 1-nitroso-2-naphthol-3,6-disulphonic acid showed good activity, but also some phytotoxicity. Thiouracil and its mixtures with p-nitrosophenol and 1-nitroso-2-naphthol displayed a particularly good activity on tobacco without being phytotoxic in the concentrations used (0.05 % + 0.05 %; Table VIII).

(4) The four nitroso compounds mentioned were used in field experiments.

In some tentative trials on French bean and broad bean the antivirus properties of p-nitrosophenol and 1-nitroso-2-naphthol were again observed (Table x). Most experiments, however, were performed on sugar beet. Indications of antivirus activity were obtained in all cases. Taking all the results obtained in 4 years (56 experiments) together, an average improvement of 7 % ± 1½ as compared with untreated plants was obtained for 1-nitroso-2-naphthol, mostly applied as its potassium salt (Graph 1). The other nitroso derivatives mentioned did not show any significant antivirus activity. The nitroso-thiouracil mixtures had a very reliable activity on tobacco, but on other plants their phytotoxicity proved to be too high (Tables XIII and XIV).

(5) It was demonstrated that these nitroso compounds only have a good effect when they are applied in a 0.1 % concentration. Two or at most three sprayings are permissible. A higher concentration or more frequent spraying produces phytotoxic effects, often to such an extent that the resulting loss exceeds the improvement brought about by the antivirus compound.

The influence of the chemical could be demonstrated with serological tests, but not with the other tests mentioned under (2). The chemical itself is decomposed in the plant. It may be that it reacts with uracil, just as thiouracil does, or with any other indispensable virus component available in the plant cells. It can thus be expected that there is not enough uracil left for the virus synthesis in the cells. As soon as the nitroso compound is entirely decomposed the uracil formed in the plant again becomes available for virus synthesis and the plant is attacked by the disease after all; only the incubation time has increased considerably. If this hypothesis should be true the nitroso compound would act as an antivirus factor. On the other hand, such a hypothesis would also explain the fact that the phytotoxic and antivirus activities of these compounds are almost the same, as the plant itself needs uracil as well.

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REFERENCES

Anonymus (BAWDEN, F. C.). 1954. *a.* World Crops **6**: 395; *b.* De Fruitteelt **44**: 674.
BARTELS, W. 1955. *a.* Phytopath. **25**: 72; *b.* ibid. **25**: 113.
————. 1956. Rev. appl. Myc. **35**: 331.
BAWDEN, F. C. 1950. Plant viruses and virus diseases. 3rd Ed. 355 pp.
————. 1954. Adv. in Virus Res. II: 31.
———— and G. G. FREEMAN. 1952. J. gen. Microbiol. **7**: 154.
———— and B. KASSANIS. 1954. *a.* J. gen. Microbiol. **10**: 160; *b.* Rev. appl. Myc. **33**: 702.
BEAL, J. M., W. H. PRESTON and J. W. MITCHELL. 1955. Plant Dis. Rep. **39**: 558.
BEEMSTER, A. B. R. and J. P. H. VAN DER WANT. 1951. Anthonie van Leeuwenhoek **17**: 285.
BLOM, L. and L. EDELHAUSEN. 1955. Analytica Chimica Acta **13**: 120.
BOOIJ, H. L., M. P. DE BRUIJN OUBOTER, M. C. CREMER and E. VAN SLOGTEREN. 1944. Meded. Inst. Rat. Suikerprod. Bergen op Zoom no. 14, or: Meded. Inst. Bloemb. Onderz. Lisse no. 73.
BRAUN, A. D., 1951. Biokhimiya (Biochemistry U.S.S.R.) **16**: 399.
BROADBENT, L. and G. D. HEATHCOTE. 1957. Rep. Rothamsted Exp. Sta. for 1956. 280 pp.
BROCK, R. D. 1952. J. AUSTR. Inst. Agr. Sci. **18**: 41.
BURGER, W. C. and M. A. STAHMANN. 1951. J. biol. Chem. **193**: 13.
CARTWRIGHT, T. E. and M. A. LAUFFER. 1954. Phytopath. **44**: 484.
CASTERMAN, C. and R. JEENER. 1955. Biochim. Biophys. Acta **16**: 433.

Casterman, C. and R. Jeener. 1956. Rev. appl. Myc. **35**: 639.
Chantrenne, H. and S. Devreux. 1958. Nature **181**: 1737.
Chiba, Y., A. Inada and I. Yoshikara. 1954. Chem Abstr. **48**: 9479.
Commoner, B. and F. Mercer. 1951. Nature **168**: 113.
Coons, G. H. 1952. Phytopath. **42**: 341.
———. 1954. J. Agric. Food Chemistry **2**: 167.
Cordon, F. M. 1953. Chem. Abstr. **47**: 11354.
Dale, J. L. and H. H. Thornberry. 1955. Illinois Acad. Sci. Transactions **47**: 65.
Davis, D. 1952. Phytopath. **41**: 301.
Duuren, A. J. van. 1955. Meded. Inst. Rat. Suikerprod. Bergen op Zoom 25, **49**: 61.
Feigl, F. 1956. Spot tests in Organic Analysis. 5th Ed. 616 pp.
Fischer, R. A. 1951. The design of experiments. 6th Ed. 242 pp.
Fraenkel Conrad, H. 1955. J. biol. Chem. **217**: 373.
Fulton, R. H. 1954. Phytopath. **44**: 489.
Gierer, A. and G. Schramm. 1956. *a*. Nature **177**: 702; *b*. Z. Naturforsch. **11b**: 138.
Goryuskin, V. A. and M. A. Kokhan 1958. Rev. appl. Myc. **37**: 430.
Gray, R. A. 1955. Phytopath. **45**: 281.
———. 1957. Phytopath. **47**: 522.
Hartman, R. T. and W. C. Price. 1950. Am. J. Bot. **37**: 820.
Helms, K. and G. S. Pound. 1955. Virology **1**: 408.
Hildebrandt, A. C., A. J. Riker and J. L. Watertor. 1952. Phytopath. **42**: 467.
Hirayama, S. 1954. Rev. appl. Myc. **33**: 120.
Hirth, L. 1953. Rev. appl. Myc. **32**: 152.
——— and J. Stolkowski. 1957. Rev. appl. Myc. **36**: 734.
Holmes, F. O. 1954. Phytopath. **44**: 492.
———. 1955. Virology **1**: 1.
Hoyle, L. 1951. Br. Abstr. A III: 685.
Howles, R. 1953. Ann. Rep. 1952 Exp. Res. Sta. Cheshunt: 26.
———. 1955. Ann. Rep. 1954 Exp. Res. Sta. Cheshunt: 25.
———. 1957. Plant Path. **6**: 46.
Hull, R. 1953. Plant Path. **2**: 39.
Jeener, R. and J. Rosseels. 1953. Biochim. Biophys. Acta **11**: 438.
John, C. A. and C. Sova. 1956. Plant Science. Biol. Abstr. **30**: 20653.
Kanngiesser, W. and B. Deubner. 1954. Arch. Ges. Virusforsch. **5**: 483.
Kasahara, M. and T. Kakumizu. 1953. Chem. Abstr. **47**: 1276.
Kausche, G. H., F. Hahn and L. Schleith. 1950. Z. Naturforsch. **5b**: 87.
Kirkpatrick, H. C. and R. C. Lindner. 1954. Phytopath. **44**: 529.
Knight, C. A. 1951. J. biol. Chem. **192**: 727.
Kurtzmann, R. H., A. C. Hildebrandt, R. H. Burris and A. J. Riker. 1957. *a*. Phytopath. **47**: 527; *b*. Agric. Chem. Oct.: 108.
Kuiper, N. H. 1952. Statistica **6**: 149.
Leben, C. and R. W. Fulton. 1952. Phytopath. **42**: 331.
——— and ———. 1953. Rev. appl. Myc. **32**: 151.
Lüdecke, W. 1954. Rev. appl. Myc. **33**: 193.
Markham, R. 1953. Adv. in Virus Res. **1**: 315.
Matthews, R. E. F. 1951. Nature **167**: 892.
———. 1952. ibid. **169**: 500.
———. 1953. *a*. ibid. **171**: 1065; *b*. J. gen. Microbol. **8**: 277.
———. 1954. ibid. **10**: 521.
——— and J. D. Smith. 1955. Adv. in Virus Res. **3**: 49.
Mercer, T. L., T. E. Lindhorst and B. Commoner. 1953. Science **117**: 558.
Milikan, D. F. and H. W. Guengerich. 1957. Phytopath. **47**: 25.
Milinko, L. 1956. Plant. Prot. **5**: 175.
Münster, J. 1955. Rev. rom. Agric. Vitic. Arboric. **11**: 57.
Nichols, C. W. 1952. *a*. Phytopath. **42**: 517; *b*. ibid. **42**: 579.
———. 1953. ibid. **43**: 555.
———. 1954. ibid. **44**: 92.
Nickell, L. G. 1950. Am. J. Bot. **37**: 829.
———. 1951. Bot. Gazette **112**: 290.
———, P. Greenfield and P. R. Barkholder. 1950. Bot. Gazette **112**: 42.

Noordam, D., T. H. Thung and J. P. H. van der Want. 1951. Tijdschr. Pl. ziekten **57**: 1.

Norris, D. 1954. Austr. J. Agric. Res. **5**: 658.

———. 1955. *a*. J. Sci. Food and Agric. **6**: 172; *b*. Z. Pfl. krankh. **62**: 638.

Nyman, V. L. 1952. Swedish patent no. 134. 163.

Overbeek, J. van. 1952. Ann. Rev. Plant Phys. **3**: 87.

Owen, P. C. 1955. *a*. Ann. appl. Biol. **43**: 114; *b*. ibid. **43**: 265.

———. 1956. ibid. **44**; 227.

———. 1957. *a*. ibid. **45**: 327; *b*. ibid. **45**: 456.

Panzer, J. D. 1957. Phytopath. **47**: 453.

Pfankuch, E. 1943. Mitt. Biol. Anst. Land- und Forstwirtsch. **67**: 46.

Porter, C. A. and L. H. Weinstein. 1957. *a*. Phytopath. **47**: 27; *b*. Contrib. Boyce Thompson Inst. **19**: 87.

Porter, F. M., B. C. Smale, W. H. Preston and J. W. Mitchell. 1957. Phytopath. **47**: 179.

Ragetli, H. W. J. 1957. Tijdschr. Pl. ziekten **63**: 245.

Rich, S. 1954. Phytopath. **44**: 503.

Roland, G. 1955. Meded. L. H. en Opzoekingsstations v.d. Staat te Gent **20**: 447.

Rumley, G. E. and W. D. Thomas. 1951. Phytopath. **41**: 301.

Russel, G. E. and A. R. Trim. 1957. Nature **179**: 151.

Ryzhkov, V. L., V. A. Smirnov and O. S. Gorodskaya. 1950. Biokhimiya (Biochemistry USSR) **15**: 220.

——— and N. K. Marchenko. 1954. *a*. Dokl. Akad. Nauk SSSR (Compt. rend. acad. Sci. URSS) **98**: 1033.

——— and ———. 1955. Rev. appl. Myc. **34**: 617.

Sardina, R. J. 1951. Bol. de Pat. Veg. y Entr. Agr. **18**: 129.

———. 1953. Rev. appl. Myc. **32**: 421.

Schlegel, D. E. and T. E. Rawlins. 1953. Phytopath. **43**: 589.

——— and ———. 1954. *a*. ibid. **44**: 328; *b*. J. Bacteriol. **67**: 103.

———, A. H. Gold and T. E. Rawlins. 1953. Phytopath. **43**: 206.

Schlösser, L. A. 1952. Phytopath. **20**: 75.

Schoene, F. 1954. Landb. Doc. **10**: 1081.

Schuster, G. 1956. Nachr. Bl. für Deutsch. Pfl. sch. d. Berlin **10**: 243.

Segretain, G. 1952. Compt. rend. de l'Acad. Sci. **235**: 1342.

——— and L. Hirth, 1956. Rev. appl. Myc. **35**: 331.

Simon, M. 1954. Landb. Doc. **10**: 1080.

Slogteren, D. H. M. van. 1955. Proc. Sec. Conf. Potato Virus Diseases Lisse-Wageningen 1954: 51.

Smith, F. E. 1951. Science **113**: 751.

Smith, K. M. 1951. Recent Advances in the Study of Plant Viruses. 2nd Ed. 300 pp.

Stoddard, E. M. 1942. Phytopath. **32**: 17.

———. 1944. ibid. **34**: 1011.

Takahashi, W. N. 1948. Science **107**: 226.

———. 1957. Phytopath. **47**: 535.

Thomas, W. D. and R. Baker. 1950. Rev. appl. Myc. **29**: 563.

Thung, T. H. 1949. Meded. L. H. Wageningen **49**, 156 pp.

———. 1952. Proc. Conf. Potato Virus Diseases Lisse-Wageningen 1951: 76.

——— and J. P. H. van der Want. 1951. Tijdschr. Pl. ziekten **57**: 173.

Tresh, J. M. 1956. Ann. appl. Biol. **44**: 608.

Wagnon, H. K. and J. A. Traylor. 1957. Agric. Chem. Oct.: 107.

Want, J. P. H. van der. 1951. Tijdschr. Pl. ziekten **57**: 72.

———. 1954. I.P.O. Meded. no. 85. 84 pp. Thesis Wageningen.

Weintraub, M., J. D. Gillpatrick and R. S. Willison. 1952. Phytopath. **42**: 417.

——— and W. G. Kemp. 1955. Can. J. Microbiol. **1**: 549.

Williams, P. H., M. Ebben, R. Howles, E. Grossbard, O. Owen and J. H. L. Messing. 1951. Rev. appl. Myc. **30**: 138.

———, ———, W. H. Read, R. J. Smith, R. Howles, J. H. L. Messing, O. Owen and D. M. Massey. 1952. Rev. appl. Myc. **31**: 222.

Williams, R. C. and H. Fraenkel Conrad. 1956. Bull. Signalétique **17**: 124561.

Zaumeyer, W. J. and H. Rex Thomas. 1953. Plant Diseases, the Yearbook of Agriculture U.S.D.A. p. 398.

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THE VEGETATION OF SCOTTISH PINE WOODLANDS AND DUTCH ARTIFICIAL COASTAL PINE FORESTS; WITH SOME REMARKS ON THE ECOLOGY OF LISTERA CORDATA

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(with collaboration of M. F. Mörzer Bruijns and S. Segal)

Joint publication of the Laboratory of Plant Taxonomy and Plant Geography at Wageningen (Belmontia II, fasc. 5) and the State Institute for Nature Conservation Research at Bilthoven (R.I.V.O.N., Communication nr. 62). [1]

(*received February 24th,* 1959)

1. Introduction

Coniferous woodland is not indigenous to the semi-humid and subatlantic temperate lowland climatic region of the Netherlands. However, extensive forests of conifers have been planted, mainly since the end of the 18th century. *Pinus sylvestris* and *Picea abies* were the main species planted up to the 20th century, but more recently *Pseudotsuga menziesii*, *Larix leptolepis*, and to a lesser extent other species have been used. In the coastal dune area, *Pinus nigra*, both ssp. *nigra* and ssp. *laricio*, is the exotic tree that is planted most frequently. From an ecological viewpoint, these forests have not so far been considered as separate plant associations. Since they were mostly lacking in faithful [2] species, they have been classified as "cultivated forest communities" under the native deciduous woodland associations, in most cases inside the *Querceto-Betuletum* (vide e.g. Mörzer Bruijns & Westhoff 1951, Westhoff 1954b, 1955, 1957).

In the course of the last century, however, some circumboreal-montane neophytes have migrated spontaneously into these artificial forests. This has also been observed nearly in Germany (Ascherson & Gräbner 1907, Hegi, Schütt 1936 etc.). So far, in the Netherlands *Goodyera repens*, *Linnaea borealis* and *Lycopodium annotinum* were known as such neophytes, though some doubt existed as to whether these species should be considered as "glacial relics". *Goodyera repens*, which was not mentioned by Oudemans (1874), was first recorded in the Netherlands in 1880 in the Leuvenum forest near Hulshorst (Prodromus Florae Batavae ed. altera I, 4, 1916); *Linnaea borealis*, not yet mentioned in the Prodromus Florae Batavae ed. altera (I, 2, 1903), was recorded first from Appelscha in 1920 and from Hoogeveen in 1928 (BEYERINCK, 1929b). BEYERINCK (l.c.) stated that the latter pine forest dated from 1888 and concluded that *Linnaea* might have established itself there after 1888. From morphological observations, he estimated the plants to be 26 years old, which means that the species must have been present in 1903, when the pine forest was only 15 years of age. On the other hand THYEN (in BUCHENAU, 1936, p. 380) observed, that nearby in Germany *Linnaea* did not occur in woodlands before the pines fruited, the species apparently being introduced by seed devouring birds; MEYER & VAN DIEKEN (1947, p. 193) suggest that the trees must be at least 70 years old before *Linnaea* occurs. At present 12 localities of *Linnaea* are known in the North Netherlands, viz. 11 in the Drenthian District (HOOGENRAAD, 1951; VAN OOSTSTROOM, 1958, in litt.) and one on the Westfrisian island of Terschelling, where it has been discovered quite recently (1958) in Scotch pine forest (WILCKE, 1958; see § 4 and table 3). Moreover, there is one locality further to the South near Hulshorst in the Guelder District (VAN OOSTSTROOM, 1958, in litt.). For *Goodyera repens*, 17 localities are recorded in the "Plantenkaartjes van Nederland" (IV, 1937, p. 214) and are distributed throughout the mainland of the country. In 1955, mr. T. SALVERDA (Groningen) discovered *Goodyera repens* for the first time on the Westfrisian islands, viz. on the island of Ameland in an artificial forest of *Pinus nigra* ssp. *nigra*. In 1957, the present authors observed the species for the first time on the island of Terschelling in two localities, one in Austrian and the other in Corsican pine forest. In relatively old pine-forests on the Dutch mainland, these neophytes are often accompanied by other species which are, in general, characteristic of coniferous forests, but also occur in the Netherlands in old deciduous woodland, e.g. *Trientalis europaea*, *Pyrola rotundifolia*, *P. minor*, *Vaccinium myrtillus*, *V. vitis-idaea*. These species, like the neophytes themselves, are considered faithful species of the phytosociological order *Vaccinio-Piceetalia* and the alliance *Vaccinio-Piceion* (see e.g. BRAUN-BLANQUET, SISSINGH & VLIEGER 1939, OBERDORFER 1957). There is some reason, therefore, to consider the artificial pinewoods of the Netherlands and adjacent Germany as a "nascent association" of this alliance, as was suggested for dwarf shrub communities of the same alliance on the Westfrisian islands by WESTHOFF (1947).

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[1] The following communication is to be regarded as a result of field work carried out during his term of office at the Laboratory of Plant Taxonomy and Plant Geography at Wageningen by Dr. V. Westhoff, which was completed by a visit to Amrum in 1958, and field work done by Dr. M. F. Mörzer Bruijns (State Forestry Service) and S. Segal (Hugo de Vries-Laboratory). The data obtained were worked out in the R.I.V.O.N. at Bilthoven by Dr. V. Westhoff in collaboration with S. Segal.

[2] Following Poore (1955 as did Barkman (1958), we replace the term "characteristic species" in the sense of the Braun-Blanquet method (= espèce caractéristique, Charakterart, kensoort) by "faithful species", as British ecologists use the term "characteristic species" in another sense.

We consider that HOOGENRAAD (1951) was wrong in designing *Goodyera repens* and *Linnaea borealis* as "glacial relics" and the same is probably true for the North-German plain. As early as 1907, ASCHERSON & GRÄBNER (p. 896) wrote about *Goodyera:* "Im nordwestdeutschen Flachlande selten, dort wie in Schleswig-Holstein und Dänemark wohl erst nach der Anpflanzung der Nadelwälder mit *Linnaea* und *Chimaphila* eingeführt. Dasselbe gilt wohl auch von dem vorkommen in den Niederlanden und Belgien und auch in der Rheinprovinz ist die Pflanze erst 1906 (abgesehen von wohl unrichtigen älteren Angaben)

aufgefunden worden". This is also the opinion of HEGI (II, 1909) and SCHÜTT (1936), and we cannot agree with MEYER & VAN DIEKEN (1947) who still consider *Linnaea borealis* in N.W.-Germany as a glacial relic.

In recent years, the number of pine forest neophytes has been further increased by the inclusion of *Listera cordata*. This small orchid had only been recorded once in the Netherlands: COMMELIN (1683, p. 82) mentioned *Listera cordata* (sub nomine *Ophris minima*, B. pin. = *Bifolium minimum* J. Bauh.) from dune valleys at Overveen near Haarlem "op opene luchtige plaatsen" (i.e. in clear, open habitat, so not in woodland); this record has been taken over by DE GORTER (1781, p. 237). No botanist ever found the species again and in later years it was considered to be no longer indigenous (at first by OUDEMANS 1874) or even an erroneous determination (Prodromus Florae Batavae, I, 4, 1916, p. 1787). However, in 1949 the species was discovered by J. WEIJER in an artificial forest of *Pinus nigra* ssp. *nigra* on the island of Ameland (WEIJER, 1949), the same forest where *Goodyera repens* occurs (see above). In 1953 it was found by J. DEELDER (State Forestry Service) in an artificial forest of *Pinus nigra* ssp. *nigra* in the Western part of the island of Terschelling; in 1955, by J. DEELDER, in similar conditions in the centre of Terschelling, and in 1956, by M. T. JANSEN and D. T. E. VAN DER PLOEG, on the island of Schiermonnikoog, again in a similar locality. Recently, *Listera cordata* has also been observed on the Dutch mainland, near Boschoord (Vledder) by G. JAGER in 1956. It was the first Dutch record in a forest of Scotch pine.¹)

As the pinewoods of Scotland are well-known to be one of the native habitats of *Listera cordata* (TANSLEY, 1949; SUMMERHAYES, 1951; CLAPHAM, TUTIN & WARBURG, 1952; etc.), we examined some Scotch pine woodlands (natural and planted,) during a trip to Scotland in 1956.

2. DISTRIBUTION AND ECOLOGY OF LISTERA CORDATA

HULTÉN (1950) assigns *Listera cordata* to his relatively small group of "boreal-circumpolar plants that are boreal-montane in Europe but with gaps in Siberia". To this group belong also *Galium trifolium*, *Botrychium lanceolatum*, *Pyrola chlorantha*, *Potamogeton filiformis*, *Isoetes tenella*, *Carex buxbaumii*, *Juncus stygius*. SUMMERHAYES (1951) lists *Listera cordata* together with two other orchids (*Gymnadenia albida* and *Goodyera repens*) as belonging to the "northern-montane" element. Several authors agree that in the Southern part of Europe the species is confined to mountains, whereas in the North it occurs also in the plains (HEGI, 1906, SUMMERHAYES, 1951, HERMANN, 1956, etc.); one may ask, however, where these Northern plains begin. Before considering this point in detail, it is necessary to look for the ecological amplitude of the species. Central European plant geographers, as well as British ecologists, have stressed, that *Listera cordata* occurs in two

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¹) During the type-setting, in May 1959, MÖRZER BRUIJNS observed Listera cordata for the first time on the island of Vlieland, near "Nieuwe Kooi", in a forest of *Pinus nigra* ssp. *nigra*, 35 years old; in June 1959, Mr. E. STAPELVELD discovered a second locality for the Dutch mainland, again in the "Drenthian district", in the nature reserve "Tonckensbos", a forest of Scotch pine near Norg.

apparently rather different habitats, viz. (1) on raw humus in damp to moist woodland, with a preference for spruce forest; (2) in open wet heather moorland and in *Sphagnum* bogs (HEGI, 1906, ASCHERSON & GRÄBNER, 1907, CLAPHAM, TUTIN & WARBURG, 1952, BUCHENAU, 1894, SUMMERHAYES 1951, RAUNKIAER, 1942, TANSLEY, 1949, HERMANN, 1956, etc.). In high Savoie (France) it has been observed in mountain pastures on S. slopes (WEIJER, 1949). Though in Central Europe the woodland habitat is damp to moist, this is not necessarily so in the colder Scandinavian climate with its smaller evaporation rate. For example PALMGREN (1922) and S. SEGAL (unpublished observations) observed *Listera cordata* there in dry as well as in moist woodland. PALMGREN even remarks, that the species may be less frequent in a relatively moist habitat. As far north as Prussia, however, *Listera cordata* is still restricted to moist and wet localities (STEFFEN 1931, GROSSER 1955).

Considering the preference of *Listera cordata* for either woodland or moorland, it has been suggested, that two ecotypes could be distinguished (SUMMERHAYES, 1951). However, as the latter author points out, the two habitats may not really be so different, since the soil is usually acid in both habitats and the small plants in the open localities usually grow in the shelter of comparatively tall heather on north-facing slopes or in the wet *Sphagnum* of raised bogs (see also METCALFE, 1950). Such an ecological amplitude suggests an oceanic, humid climate, in which the difference between the microclimates in and outside the woodland is less pronounced than in a more continental and drier climate. It is strange, therefore, that OBERDORFER (1949) describes the area of *Listera cordata* as "subarctical-boreal-(continental)", whereas BUCHENAU (1936), writing from a somewhat local point of view, mentions it as "atlantic". Since *Listera cordata* is common both in Norway and Sweden (HULTÉN, 1950) and fairly common not only in the Northern half of Britain, but even throughout Ireland (PRAEGER, 1934; SUMMERHAYES, 1951) the qualification "continental" is puzzling.

It is remarkable that Central European plant sociologists (BRAUN-BLANQUET, SISSINGH & VLIEGER 1939, OBERDORFER 1949, 1957) still seem to neglect the open (moorland) habitat of *Listera cordata* and consider it a characteristic woodland species, viz. a faithful species of the alliance *Vaccinio-Piceion* or (OBERDORFER 1957) of the order *Vaccinio-Piceetalia*. Since *Listera cordata* occurs frequently in both the woodland and moorland habitats in Britain and Denmark (TANSLEY 1949, SUMMERHAYES 1951, RAUNKIAER 1942), whilst in Ireland the species is confined to the latter type (except for one record in a *Taxus* woodland; PRAEGER 1934, WEBB 1943, TANSLEY 1949), it seems that in Central Europe *Listera cordata* is much rarer in the "open" habitat than in woodland, whereas nearer to the boreo-atlantic coast there is a gradual increase in its preference for the open habitat. WEIJER (1949) mentioned, however, that in High Savoie (French Alps) *Listera cordata* was found in mountain pastures only. It is also remarkable, that Central European plant geographers stress that *Listera cordata* is limited to a true shadowy, woodland microclimate and that it disappears when the wood had been thinned (Hegi 1906, p. 388; Buchenau 1894, p. 538). On the contrary Summerhayes (1951, p. 173), in Britain, observed a preference for open habitat within woodland, the species evading dense shade.

In France (Fournier 1946) and in Germany, except for the NW. plains (Hegi, 1909), *Listera cordata* is still restricted to the mountains. In England, however, it occurs in the lowland region too; in Ireland it descends to 10 m above sea level (Praeger, 1934), as might be expected in an extremely oceanic climate. In Denmark (11 localities, fide Hultén, 1950) it occurs also in the lowland, not only in probably artificial coniferous forest (see below), but also in bogs, where it is undoubtedly native (Raunkiaer, 1942).

Steffen (1931), in his description of the vegetation of East Prussia, designated *Listera cordata* as a very faithful ("besonders charakteristische") species of the "Fichtenzwischenmoore", i.e. a moist spruce woodland with a bog character. Though it appears from his table 25 that *Listera cordata* is absent if *Carex* species tend to dominate — when the swamp aspect thus predominates over the woodland aspect— it is clear that this habitat of *Listera cordata* presents a transitional community between the two major habitats previously mentioned: moorland and woodland.

In Belgium *Listera cordata* has been observed only once in the jurassic (mountain) district, but there is some doubt whether the locality of this specimen is reliable (Lawalrée & Vandenberghen, 1946).

There has been some controversy as to the question, whether in the N.W. plains of Germany *Listera cordata* is native, or a neophyte which became established after the artificial coniferous afforestation during the last 150 years. Ascherson & Gräbner (1907) give the latter hypothesis, but Hegi (1909) states that in the Northern German plains *Listera cordata* has been found also in bogs and moorland; however, Buchenau (1894, 1936) and Meyer & van Dieken (1947) do not confirm the latter statement.[1])

A rather special habitat is mentioned by Summerhayes (1951, p. 204), viz. "quite open . . . . , damp marshy places among sand dunes near the sea", where *Listera cordata* has been found together with *Listera ovata* and *Corallorhiza trifida!* This refers to Britain, but it is also an indication, that Commelin (1683), who mentioned the species from open dune valleys on the Dutch coast, might have been right.

In this connection it is interesting to know that *Listera cordata* occurs in a similar habitat on the North-Frisian island of Amrum, where it has been observed in a damp dune valley (Christiansen, 1953). Here the species occurs spontaneously in a natural habitat, outside of conifer plantations. The locality, the only native one yet known in the lowland of Germany, may be considered as a southern outpost of the Scandinavian area. In 1958, the author had the opportunity to visit the spot. *Listera cordata* appeared to grow here in a dune moorland on acid sand soil, under and between tall plants of *Calluna vulgaris*, *Erica tetralix*, *Empetrum nigrum* and *Vaccinium uliginosum*. The ecological situation presented a striking resemblance to that in the moors of the Scottish highlands (see below). On the other hand, the vegetation was quite similar to that of moist dune heather formation on the Westfrisian island of

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[1]) In May 1959, the author visited one of the two localities of *Listera cordata* in the "Land" Rheinland-Westfalen, viz. Einsiedelei near Olpe in Sauerland, in the lower mountain zone; they are the most Northern outposts of the Central European area of the species. The habitat of the visited spot, a primeval birch swamp (Betuletum pubescentis), is a remarkable one and reminds some Scottish and Scandinavian habitats of *Listera cordata* (see below).

TABLE I

Dune valley moorland, habitat of Listera cordata, North Frisian island of Amrum, Germany

Number of record	1	2
Year	1958	1958
Date	19/6	21/6
Shrub + Herb layer, degree of dominance in %	90	100
Moss layer, degree of dominance in %	10	60
Surface studied, in m²	15	10
Listera cordata	1.2	+.1
Dwarf shrub species:		
Empetrum nigrum	4.2–3	3.3
Salix repens	3.2	2.2
Calluna vulgaris	3.2	2.2
Erica tetralix	2.2	2.2
Vaccinium uliginosum	2.2	2.2
Genista anglica	+.1	+.2
Betula pubescens	+.1	+.2
Herbs, grasses, mosses:		
I. Indicators of heaths, moorland and acidic grassland (Nardo-Callunetea, Nardo-Galion saxatilis):		
Molinia coerulea	2.2–3	3.2
Potentilla erecta	+.1	+.1
Luzula campestris var. congesta	+.1	1.1
Pedicularis sylvatica	+.1	(+)
Galium saxatile	—	+.2
Dicranum scoparium	—	2.3
Pleurozium schreberi	—	1.2
II. Other grassland indicators:		
Festuca ovina ssp. capillata	+.2	2.2
Anthoxanthum odoratum	1.1	1.1
Festuca rubra	+.2	—
Rumex acetosa	—	+.1
III. Swamp indicators (Scheuchzerieto-Caricetea fuscae, Caricetalia fuscae, Caricion canescentis-fuscae):		
Eriophorum angustifolium	2.1–2	2.1
Carex echinata	—	+.1
Viola palustris	—	+.1
IV. Bog indicators (Oxycocco-Sphagnetea):		
Oxycoccus paluster	—	2.2
Sphagnum papillosum	+.2	—
V. Hygrophyte companions (± indifferent):		
Pseudoscleropodium purum	1.2	3.3
Pohlia nutans	+.2	—

Terschelling. This may be shown by two sample plot analyses (records), made by the author on the Amrum locality and given in table 1. The only species of this table which are wanting in the dune moorland of Terschelling are *Oxycoccus paluster* (there replaced by *Oxycoccus macrocarpus*) and *Listera cordata!* In comparing the two records of table 1 it is obvious that the rate of abundance and sociability of *Listera cordata* is higher in the first record. This may be due to the much denser moss cover in the second record, in combination with a dense dwarf shrub layer. Since at present *Listera cordata* thrives abundantly in artificial pine forests on the Dutch Westfrisian islands, it may be expected that the species will establish itself here also in the more natural conditions of the wet dune valleys. This seems much more probable than a movement southwards since (1) *Listera cordata* is acidiphilous and the dunes in Holland S. of Alkmaar are rich in lime ("Dune district") but N. of Alkmaar poor in lime ("Wadden district"); and (2) most of the wet dune valleys in the Dune district have been drained.

Considering the woodland habitat, we may ask in what type of woodland is *Listera cordata* likely to occur. In the Alps and the Central European secundary mountain-chains, there is a marked association with the subalpine *Picea*-forest, and to a lesser extent with the montane *Abies-Picea*-forest. BRAUN-BLANQUET, SISSINGH & VLIEGER (1939) mention it as a constant and faithful species in the *Listera cordata-Hylocomium umbratum*-woodland association in the Jura (1200–1500 m alt.) on calcareous subsoil, in the *Piceetum subalpinum* in the Alps (1200–1800 m. alt.), and in the *Picea excelsa-Hieracium rotundatum*-association in the Eastern Carpathes, whereas it occurs with a lower presence degree as a faithful species in the *Piceetum tatricum* (N. Tatra 1100–1200 m alt., S.-Tatra 1500–1650 m alt.) and in the *Mastigobryeto-Piceetum* in the Black Forest (600–1000 m alt., confirmed by OBERDORFER, 1957); all these associations belong to the subalpine sub-alliance *Rhodoreto-Vaccinion.* In all these mountains, *Listera cordata* appears to be absent from pine-woods (*Pinus sylvestris*, *P. cembra*, *P. nigra*, *P. mugo*). AICHINGER (1949), in a study of the succession types of Central-European woodland communities, comes to a similar conclusion, for he finds *Listera cordata* to be a characteristic spruce forest species and he mentioned it only once from a pine forest ("*Pinetum silvestris-basiferens*") (l.c. p. 90) in the Eastern Alps near Villach. He comments that this forest is really a secondary pioneer community, rejuvenated after the cutting down of a spruce forest and has a tendency to develope into a spruce forest again. However, in the Eastern Pyrenees, *Listera cordata* appears to be a faithful species of the *Rhododendron ferrugineum-Listera cordata*-association, in which *Pinus mugo* is the dominant tree (BRAUN-BLANQUET c.s. 1939). In view of the association of the species with pine woods in Scotland, it is possible that this Pyrenean association is of a more oceanic character. — In the montane Central European sub-alliance *Abieto-Piceion*, *Listera cordata* seems to be much rarer; it has been mentioned only in the *Aremonieto-Piceetum* of Yougoslavia (BRAUN-BLANQUET c.s. 1939) and in the *Galio-Piceetum* of the Eastern Black Forest (OBERDORFER, 1957).

The woodlands of Northern Europe are united by BRAUN-BLANQUET c.s. (1939) into the sub-alliances *Piceion septentrionale* and *Phyllodoco-Vaccinion; Listera cordata* has been observed mainly in the former. The *Piceion septentrionale* does not only include coniferous woodland, but also the boreal-subalpine and sub-arctic deciduous forest, mainly birch forests. HULTÉN (1950) describes the Scandinavian habitat of *Listera cordata* as "fugtig barrskog" (wet coniferous woodland), and BARKMAN (1951) informs us that *Listera cordata* in N.-Sweden is "more or less restricted to spruce forest". Nevertheless, BRAUN-BLANQUET c.s. (1939), following KUJALA (1929), mention *Listera cordata* as a constant and faithful species of the *Betuleto-Vaccinietum lapponicum*, a birch woodland type occurring to the North of the spruce-limit between 69° and 69°30′ (see also BEYERINCK, 1936). The species is also present in the Scandinavian spruce forest, *Piceetum fennoscandicum*, and in the *Pineto-Vaccinietum myrtilli arctostaphyletosum*, which occurs in Sweden, Finland and Estland and is essentially a Scots Pine forest. Moreover, SJÖRS (1949) reports that *Listera cordata* has been observed in an alder wood (*Alnus glutinosa* x *incana*) in Dalarna, Sweden.

Within the sub-alliance *Phyllodoco-Vaccinion*, *Listera cordata* occurs in the *Hylocomieto-Betuletum tortuosi*, a wide-spread Scandinavian mountain birch woodland on very acid raw humus. BRAUN-BLANQUET, SISSINGH & VLIEGER (l.c.) mention it only in the relatively oceanic subassociation *Hylocomieto-Betuletum tortuosi cornetosum*, with presence degree I, based on Norwegian and Finnish records from NORDHAGEN and KUJALA. SEGAL (in litt.) made a record of it near Björkliden, Sweden (1957, 450 m alt.) with some plants of *Listera cordata* in it.

In Scotland, *Listera cordata* occurs occasionally in the Caledonian pine forests of the Highlands (TANSLEY 1949, SUMMERHAYES 1951) and in Highland birchwoods, e.g. in Caithness (id.); as well as in tall *Calluna* and *Vaccinium* moorland vegetations, in damp or moist habitats and above the timber line, e.g. in the Cairngorms (METCALFE, 1950).

From these data it is obvious, that the woodland habitat (Scots pine and birch) of *Listera cordata* in Scotland corresponds more closely to that of Scandinavian than to that of Central Europe.

3. SCOTTISH PINEWOOD

During an excursion in Scotland from 29th June to 5th July 1956 we had the opportunity to see some pinewoods. Sample plot analyses records after the BRAUN-BLANQUET method were made as follows:

1. Near Fochabers, less than 200 ft (70 m) altitude. Spontaneous pinewood, age ca. 100 years, 15 m high. 30-VI-1956.
2. Culbin Sands, N. coast of Morayshire. Sea sand dunes, fixed from 1921–1951 by afforestation (OVINGTON, 1950; see also Anon., 1953). Forest of *Pinus nigra* ssp. *laricio*, age 45 years, 15–20 m high, I-VII-1956.
3. Currwood near Dulnanbridge, between Inverness and Aviemore, ca. 700 ft. (230 m) alt. Pinewood, regenerated after destruction (by fire?), several times thinned, not pastured. Age ca. 80 years, 18 m high. 1-VII-1956.

4, 5. Part of the Abernethy Forest adjoining Loch Garten near Aviemore, ca. 800 ft (270 m) alt. Old native pinewood, regenerating spontaneously. Open canopy of Scots pines, 20 m high, age ca. 200 years, alternating with groups of younger pines in varying ages, up to ca 10 m high. We were informed by the Nature Conservancy, Scotland, that this forest represented a characteristic example of group regeneration of pine at all size stages, showing the formation of dense thickets in the neighbourhood of parent trees and the natural thinning of these thickets. The pines have regenerated actively on a heather area not recently burned. This small piece of forest has attained the structure at which the Conservancy's management of pine forest is aiming in the first instance and but for any catastrophe, such as fire or wind-blow, it should maintain itself indefinitely. Pine forest with this structure is extremely rare, even in Scandinavia. The moss mat and fermentation layers are not as thick or dense as in the normal forests of these types which follow fire. 1-VII-1956.

6. Cairngorms National Nature Reserve near Aviemore, ranging from 840 ft (260 m) in altitude to 4296 ft (1309 m). The splendid Scots pine woodland still found here is, as the Nature Conservancy, Scotland, kindly informed us, the largest surviving area of the ancient Caledonian Forest, parts of which are still self-regenerating and contain their naturally associated flora and fauna. One of our analyses has been made in an open apparently primeval woodland on glacial drift, at Loch an Eilein near Rothiemurchus, a forest not managed since time immemorial. Old pines ca. 300 years of age, with heavy round crowns and far apart, alternated with younger trees of between 200–40 years old. Our second analysis was not made in a primeval woodland, but, on a west exposure on glacial drift, in a naturally regenerating forest of Scots pine, cut down (or blown down?) ca. 80 years ago and with no record of a fire. Besides the species mentioned in our analyses (see table), some other characteristic pine wood species occur in the Reserve, viz. *Linnaea borealis*, *Pyrola media* and very rarely *P. uniflora* (information by the Nature Conservancy). *Listera cordata*, however, was not mentioned nor was it seen by us here. 2-VII-1956.

The pine forest of the Cairngorms has also been described by TANSLEY (1949, p. 447–449) under the name "Rothiemurchus Forest".

7. Kinlochewe Forest near Beinn Eighe at the W.-coast of Scotland, county Ross and Cromarty. Altitude ca. 1000 ft (300 m). 3-VII-1956. In this extreme oceanic climate the annual precipitation attains one of the highest values in the United Kingdom (ca. 70 inches = 2540 mm), whilst the number of mean annual hours of bright sunshine (less than 1200) is very low; the W.-winds are very strong and continuous. Nevertheless, the natural climax of the region would be a pine forest mixed with deciduous trees and it is mainly by overgrazing by red deer and sheep that woodland has become very scarce and its regeneration difficult. Our analysis was made on a N.-exposure on a very poor soil with a wet podsol profile (30 cm. raw fermentation layer, 20–30 cm. bleached sand layer). As in the Cairngorms, the tree layer consisted of some 200–300 years old Scots

pines, ca. 30 m high, and between them trees of 150–100 years, 80–40 years, shrubs and saplings. Dr. D. Mc Vean (The Nature Conservancy, Scotland), who studied this woodland thoroughly, kindly showed us a characteristic locality, so that nearly all species occurring in it would occur in our analysis. Dr. Mc Vean also informed us that *Pyrola*-species do not occur here; they are confined to woodland on richer soils.

The Kinlochewe Forest has also been described by Tansley (1949, p. 450) under the name "pine-forest on the south-western shore of Loch Maree".

Comparing the analyses made in these localities, it became clear that the Highland pine woods of Currwood, Abernethy Forest, Cairngorms Reserve and Benn Eighe had a great similarity with respect to floristic composition, history, structure of vegetation and altitude, whereas the forests of Fochabers and Culbin Sands, both at lower altitudes, differed considerably form the former. Therefore, 6 analyses of the former woodland type are combined in table 2. A sample list of the forest of Ballochbuie at Balmoral, taken from Tansley's (1949) description of the Caledonian Pine Forest, has been added to the table as nr. 7. The description of the Highland Scots pine woodland type by Tansley suggests that nearly all important localities where this type survives are represented in our table.

Tansley (l.c.) points out, that the Caledonian Highland pine wood has to be considered a somewhat impoverished Southwestern outpost of the Fenno-scandinavian coniferous woodlands. In comparing table 2 with the vegetation tables of the boreal sub-alliance *Piceion septentrionale* (alliance *Vaccinio-Piceion*, order *Vaccinio-Piceetalia*) by Braun-Blanquet, Sissingh & Vlieger (1939), it is clear, indeed, that the Highland pinewood fits very well into this sub-alliance. Braun-Blanquet c.s. (l.c.) only present a short remark on the Scottish pinewoods (p. 67–68). They do not give a table of it, but consider them to be either a sub-association of the *Pineto-Vaccinietum myrtilli* or, more probably ("wohl eher aber"), a special association. Curiously enough, they state in their general outline (l.c., p. 5) that the order *Vaccinio-Piceetalia* does not occur in the humid region of Western Europe!

Compared to the Fennoscandian associations of the sub-alliance, the Scotch pinewood appears to be slightly poorer because of (1) the absence of *Picea abies*, *Lycopodium complanatum* and *Pyrola chlorantha*, which are not native at all in Britain (Clapham, Tutin & Warburg, 1952); (2) the absence of *Lycopodium selago*, *Empetrum hermaphroditum*, *Vaccinium uliginosum* and *Lophozia lycopodioides*, because in Scotland these species do not occur in woodland, but in open moorland (Clapham, Tutin & Warburg, 1952; Macvicar, 1912), apparently as a consequence of the oceanic climate (cf. § 2). On the other hand, the Scotch pinewood contains at least two geographically differential eu-atlantic species, viz. *Carex binervis* and *Erica cinerea*. According to Hultén (1950) both occur also in the extreme S.W. part of Norway, so that it may be expected, that in Western Norway a gradual transition may be observed between the Scottish pinewood type and the *Pineto-Vaccinietum myrtilli*. The presence of *Betula pubescens* ssp. *odorata*

(Bechst.) E. F. Warburg and *Populus tremula* constitutes a difference between boreal and alpine coniferous woodland; these species are given in table 2 as differential species of the sub-alliance *Piceion septentrionale*, according to BRAUN-BLANQUET, SISSINGH & VLIEGER (1939.)

A faithful, characteristic species of the Scottish pinewood is the dominant *Pinus sylvestris* ssp. *scotica* (Schott) E. F. Warburg, which seems to be a Scottish endemic. We are not quite sure, however, that there exists a real difference between this taxon and the *Pinus sylvestris* of Norway and Sweden. For this reason and for the possibility of a gradual transition between the Scottish pinewoodland type and the *Pineto-Vaccinietum myrtilli* in S.W.-Norway (see above), we think it better not to describe as yet the Scottish pine woodland type as a new association. Provisionally we consider it as an atlantic vicariant of the *Pineto-Vaccinietum myrtilli* (*Pineto-Vaccinietum myrtilli atlanticum*).

For the sake of comparing the Scandinavian records with those of Scotland we present next vegetation record of a *Pineto-Vaccinietum myrtilli* forest near Hån (S.-Sweden), made and kindly offered to us by Mr. S. SEGAL.

Date: 30th August 1952. Surface studied: 300 m².

Tree layer: height 12 m, degree of dominance 80–90 %:			
Pinus sylvestris (ssp.?)	4.1	Picea abies	2.1
Shrub layer: height to 40 cm, degree of dominance 20 %:			
Vaccinium myrtillus	2.2–3	Calluna vulgaris	+.2
Vaccinium vitis-idaea	1.2		
Herb layer: 30 %			
Listera cordata	+.1	Dryopteris linnaeana	+.2
Goodyera repens	+.2	Melampyrum sylvaticum	1.2
Pyrola minor	1.1	Solidago virgaurea	+.1
Pyrola chlorantha	+.1	Festuca ovina	+.2
Ramischia secunda	+.1–2	Deschampsia flexuosa	+.2
Linnaea borealis	2.2	Rumex acetosa	+.1
Lycopodium annotinum	1.2	Stellaria sp.	+.1
Trientalis europaea	2.2		
Moss layer: 40 %			
Ptilium crista-castrensis	+.2	Pleurozium schreberi	2–3.2
Hylocomium splendens	1–2.2	Dicranum scoparium	2.2
Hylocomium spec.	1.2	Peltigera cf. aphtosa	+.2

Mr. SEGAL emphasizes the fact that the habitat was a dry one.

According to WHITE (1898, cit. in TANSLEY, 1949) in Scotland the following herb species may be confined to this community: *Goodyera repens*, *Corallorhiza trifida* and *Pyrola uniflora;* TANSLEY adds that these species are on the whole rare, which may be the reason why only *Goodyera repens* is represented in our table. The four taxa *Pinus sylvestris* ssp. *scotica*, *Goodyera repens*, *Corallorhiza trifida* and *Pyrola uniflora* may be considered faithful species of the community. WHITE (l.c.) also gives a number of herbs characteristic of (but not confined to) the *Pineto-Vaccinietum atlanticum;* four of them (*) occur in our table 2:

Linnaea borealis
* Listera cordata
Pyrola media
* Pyrola minor
* Pyrola rotundifolia
Pyrola secunda
* Trientalis europaea

These species occur also in birch woodland or in open moorland. It is possible, however, that some of them will present a presence optimum in the *Pineto-Vaccinietum atlanticum*, so that they may be considered faithful species of this community; this cannot be concluded on the base of the available data.
We are therefore giving the (*) species in table 2 as faithful species of the alliance, order and class, according to the classification by Oberdorfer (1957). We also put into these categories those species (phanerogams and mosses), which in the whole of their area have to be considered as such, although they (at least the phanerogams) may show no preference for pinewood in the Highlands: *Vaccinium myrtillus*, *V. vitis-idaea* and *Arctostaphylos uva-ursi.*

It is probable, that within the *Pineto-Vaccinietum atlanticum* several subassociations and (or) variants may be distinguished, e.g. a unit on poor soil lacking *Pyrola* ssp. (see also § 2) and the species indicating mild humus (*Viola riviniana*, *Luzula pilosa*), but rich in *Sphagnum* ("*sphagnetosum*"), and a unit with *Pyrola*, *Viola*, *Luzula pilosa*, but with less or no *Sphagnum* ("*pyroletosum*"). The present material, however, does not allow us to make such a distinction on the basis of table 2. It may appear from this table, that *Listera cordata* is present both in the poor "*sphagnetosum*" (record nr. 6) and in the richer variant (list from Tansley), but this is not certain, as in the latter list *Sphagnum* was abundant too.

The two other pinewoods visited by us situated in the lowlands, viz. at Culbin Sands and near Fochabers, do not belong to the *Pineto-Vaccinietum atlanticum.* The artificial Corsican pine afforestation at Culbin Sands showed such an interesting and striking resemblance with the artificial Corsican and Austrian pine afforestations on the Dutch Westfrisian islands, that it will be dealt with in § 4 (see table 3, nr. 7); *Listera cordata* occured there. In the Scots pine forest at Fochabers (< 70 m alt). the following record was made by us:

200 m^2. Tree layer: age ± 100 years, 15 m high.
Pinus sylvestris (ssp. scotica?) . . 3.1

Herb layer: 100 %

Pteridium aquilinum	4.5	Agrostis stolonifera	+.2
Erica cinerea	3.2	Veronica officinalis	+.2
Deschampsia flexuosa	2.2	Galium hercynicum	+.2
Lonicera periclymenum	2.2	Rubus fruticosus	+.2
Solidago virgaurea	1.1	Fagus sylvatica, iuv.	r
Viola riviniana	1.1	Acer pseudoplatanus, iuv.	r
Teucrium scorodonia	1.2		

Moss layer: 20 %

Pleurozium schreberi	2.3	Hylocomium splendens	+.2
Pseudoscleropodium purum	+.2		

Conspicuous differences with the *Pineto-Vaccinietum atlanticum* are: (1) the absence of some constant characteristics of the latter association, viz. *Vaccinium myrtillus*, *V. vitis-idaea*, *Trientalis europaea*, *Blechnum spicant*, *Melampyrum* spp., *Rhytidiadelphus triquetrus;* (2) the dominance

TABLE II

Pineto-Vaccinietum myrtilli atlanticum

Highland Scots Pine wood community.
Analyses: June–July 1956.
Alliance: Vaccinio-Piceion.

Sub-alliance: Piceion septentrionale.
Order: Vaccinio-Piceetalia.
Class: Vaccinio-Piceetea.

Cu = Currwood
AF = Abernethy Forest
Cai = Cairngorms

BE = Benn Eighe
Ba = Ballochbuie

M = Mörzer Bruijns
W = Westhoff
T = Tansley
u = unknown

Quantitative data in nrs. 1-6 after the scale of Braun-Blanquet, in nr. 7 after the British method.

Number	1	2	3	4	5	6	7
Locality	Cu	AF	AF	Cai	Cai	BE	Ba
Author	M	M	W	M	W	M	T
Date	1 VII	1 VII	1 VII	2 VII	2 VII	3 VII	—
Altitude in meters	230	270	270	>350	>350	300	>350
Tree layer(s), age in years	80	200	200	300	80	250	150
	—	—	±50	200	u	150	u
	—	u	—	80–40	u	80–40	u
Tree layer(s), height in meters	18	20	22	12–15	15–18	30	18
	—	2–10	4–10	5–10	u	20	u
						4–10	
Tree layer(s), degree of dominance in %	70	50	90	40	70	50	u
	—	10	10	20	—	20	
Shrub layer, height in meters	<1	—	1–3	—	<1	—	u
Herb layer, degree of dominance in %	60	70	90	100	100	70	u
Moss layer, degree of dominance in %	90	90	60	80	100	100	u
Surface studied, in square meters	300	250	300	250	250	500	u
Faithful species of the community:							
Pinus sylvestris ssp. scotica, upper tree layer	4.1	3.2	5.1–2	3.1	4.1	3.1	d
Idem, lower tree layer	—	+.2	+.1	2.1	—	2.1	—
Idem, shrub layer	—	—	+.1	—	—	—	—

Differential species of the sub-alliance (compared with alpine communities):							
Betula pubescens ssp. odorata, lower tree layer	—	—	+.1	+.1	—	+.1	oc
Idem, shrub layer	+.1	—	+.1	—	—	—	—
Populus tremula	—	—	+.1	—	—	—	loc
Faithful species of the alliance:							
Melampyrum pratense ssp. + M. silvaticum	+.2	+.2	+.1–2	1.1	+.1–2	+.1	sp
Plagiothecium undulatum	+.2	—	—	—	+.2	1.2	f
Dicranum majus	—	—	—		1.2–3	1.3	o–f
Sphagnum girgensohnii	—	—	—	+.3	+.2	—	va
Sphagnum quinquefarium	—	—	—	—	—	2–3.4	—
Faithful species of the order:							
Trientalis europaea	2.1	+.1	+.1	+.1	+.1	—	—
Rhytidiadelphus loreus	—	—	—	—	+.2	2.2	ab
Ptilium crista-castrensis	—	—	2.3	—	—	+.2	fr
Listera cordata	—	—	—	—	—	+.2 [2])	sp
Faithful species of the class:							
Vaccinium myrtillus	1.3	3.3	4.4	3.3	5.4	3.3	ld
Vaccinium vitis-idaea	+.2	1.1	2.2	3.3	1.1–2	2.2	ld
Pyrola rotundifolia	—	—	+.2	—	—	—	—
Pyrola minor	—	—	—	+.1	—	—	—
Arctostaphylos uva-ursi	—	—	+.3	—	—	—	—
Companion species, occurring more than once:							
Deschampsia flexuosa	3–4.4	2.2	2.2	2.3	1.2	2.2	lf
Calluna vulgaris	1.3	3.4	3.3–4	1.2	+.2	3.3	ld
Sorbus aucuparia	1.1	+.1	1.1	+.1	+.1	1.1	oc
Hylocomium splendens	3.3	3.3	2.3	3.3	4.4	4.4	ab
Galium hercynicum	2.2	+.2	+.2	2.2	—	1.2	sp
Blechnum spicant	+.3	—	+.2	+.1	+.2	+.2	sp
Luzula pilosa	1.2	+.2	1.1–2	1.2	+.2	—	sp

TABLE II *(Continued)*

Number	1	2	3	4	5	6	7
Rhytidiadelphus triquetrus	3.3	3.3	3.3–4	3.3	3.3–4	—	ab
Oxalis acetosella	+.2	+.2	+.2	+.2	—	—	sp
Potentilla erecta	+.1	+.2	+.2	+.1	—	—	sp
Pleurozium schreberi	3.3	3.3	+.2	—	—	2.3	fr
Juniperus communis	—	1.2	2.1–2	2.1	+.1	+.1	—
Viola riviniana	—	+.2	+.2	+.1	—	—	sp
Dicranum scoparium	2.2	—	—	2.2	—	1.3	f
Polytrichum commune	1.3	—	—	+.2	—	—	oc
Pteridium aquilinum	—	—	—	2–3.3	+.2	2.3	—
Molinia coerulea	—	—	—	—	+.2	+.2	sp
Veronica officinalis	+.1	—	+.2	—	—	—	sp
Luzula congesta	+.1	—	—	+.2	—	—	sp
Holcus mollis	+.1	—	—	—	—	—	lf
Dryopteris phegopteris	—	—	+.2	—	—	—	sp
Dryopteris spinulosa	+.1	—	+.1	—	—	—	—
Agrostis canina	—	—	+.2	—	—	—	sp
Equisetum silvaticum	+.1	—	—	—	—	—	sp
Rumex acetosella	—	—	—	+.1	—	—	l
Anthoxanthum odoratum	—	—	+.1–2	+.1	—	—	—

Besides, next species were noted once:

in nr. 3: Anemone nemorosa, Lathyrus montanus, Athyrium filix-femina, Carex nigra, Pseudoscleropodium purum;

in nr. 6: Empetrum nigrum, Quercus robur iuv., Pleurochaete squarrosa (fide Dr. D. Mc Vean), Thuidium tamariscinum;

in nr. 7: Deschampsia caespitosa, Solidago virgaurea, Polystichum aculeatum, Luzula silvatica, Juncus squarrosus, Nardus stricta, Euphrasia sp., Hieracium sp., Mnium hornum, Campylopus flexuosus, Sphagnum sp.

N.B. As to the large number of accidental species in nr. 7, it should be kept in mind that the author of this list, Sir Arthur Tansley, did not mention the surface studied, but that probably (according to the method used by him) this surface was very much larger than ours.

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1) Tansley did not indicate Carex binervis, but C. distans; perhaps he was mistaken.
2) Not seen by us, but locality indicated by Dr. D. Mc Vean within the surface studied by us.

of *Pteridium aquilinum;* (3) the occurrence of some typical lowland [1]) forest species, viz. *Lonicera periclymenum* and *Fagus sylvatica;* (4) the absence of all faithful herbs of the *Pineto-Vaccinietum atlanticum.* The Fochabers community bears hardly any resemblance to the order of *Pinetalia* (OBERDORFER, 1957), except perhaps for the hercynic association "*Pinetum variscum*". Somewhat more striking is the resemblance with the montane Central-European *Luzulo-Fagion* alliance, the beech woodland on acid soil.

4. THE PINE AFFORESTATIONS ON COASTAL DUNE SAND ON THE DUTCH WESTFRISIAN ISLANDS AND CULBIN SANDS, SCOTLAND

For understanding and interpreting the secundary vegetation of artificial pine forests on dunes, it is necessary to know the habitat and the vegetation (1) before afforestation and (2) in the dune area adjacent to the forest. A knowledge of (2) enables one to make some estimate of the former conditions which is particularly valuable if these are not known by direct observation (as in the present case). Moreover, dune species will continue to send diaspores into the forest, thus creating or maintaining there a temporary or permanent secundary population ("vicinism" sensu NORDHAGEN. 1939). The number of these migrating species will decrease gradually from the margin to the interior of a forest.

The flora and vegetation of Terschelling have been studied by VAN DIEREN (1934) and WESTHOFF (1943, 1947); the vegetation of Ameland by BRAUN-BLANQUET & DE LEEUW (1936); that of Schiermonnikoog by DEN HARTOG (1952) and WESTHOFF (1954a); and that of Culbin Sands by OVINGTON (1950). The vegetation records of all Westfrisian islands has been summarized by WESTHOFF in MÖRZER BRUIJNS & WESTHOFF (1951); the plant communities with woody species (lignosa) found in the Dutch dune area (incl. the Westfrisian islands) and its inner border have been described by WESTHOFF (1953); and the Dutch dune grasslands by BOERBOOM (1958). The forestry aspects of dune afforestation on the Westfrisian islands have been reported by BOODT (1934).

The dune sand of the islands and the adjacent Dutch dune continent ("Waddendistrict") is poor in lime (< ± 1 %, on Terschelling even < 0,2 %), in contrast to the Southern "Dune District" (lime content ± 3 – ± 20 %). From Terschelling to the East, the lime content gradually increases in such a way that the flora of Schiermonnikoog has certain affinities with that of the Dune District. All islands have both a hygrosere, in the wet dune valleys, and, on the dunes, a xerosere which is independent of the phreatic water. In both seres the dunes have been partly afforested so that the wet dune valleys were drained, especially on Terschelling, and have continued to dry up as transpiration by the growing pine plantations increased.

The xerosere as far as it relates to our subject is illustrated by

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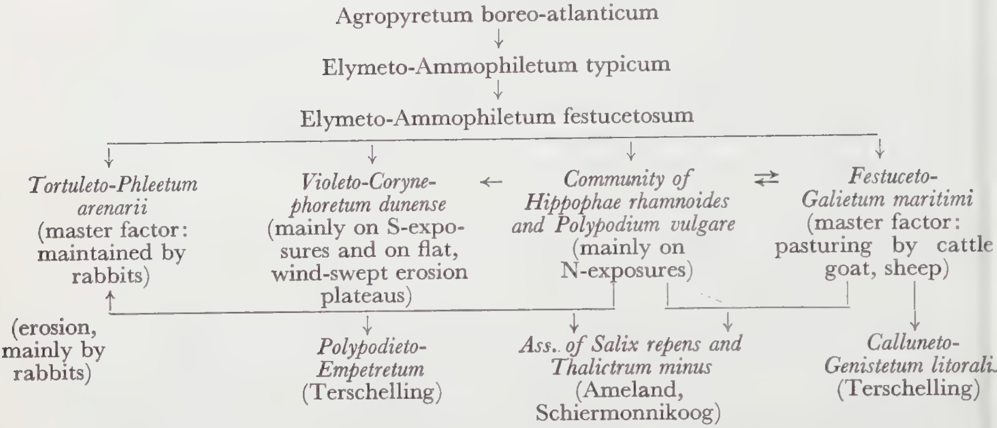
[1]) Only as regard Scotland.

SCHEME I

Xerosere on the Westfrisian islands


Agropyretum boreo-atlanticum
Elymeto-Ammophiletum typicum
Elymeto-Ammophiletum festucetosum
Tortuleto-Phleetum arenarii (master factor: maintained by rabbits)
Violeto-Corynephoretum dunense (mainly on S-exposures and on flat, wind-swept erosion plateaus)
Community of Hippophae rhamnoides and Polypodium vulgare (mainly on N-exposures)
Festuceto-Galietum maritimi (master factor: pasturing by cattle goat, sheep)
(erosion, mainly by rabbits)
Polypodieto-Empetretum (Terschelling)
Ass. of Salix repens and Thalictrum minus (Ameland, Schiermonnikoog)
Calluneto-Genistetum litorali (Terschelling)

scheme I. The names of the communities in which afforestation has taken place have been printed in italics.

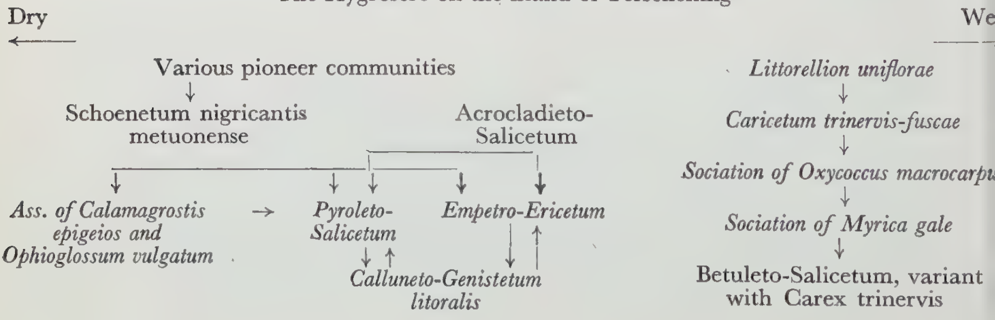
On Terschelling, the *Festuceto-Galietum maritimi* is not extensive and is only of minor importance. It has not been used for afforestation; in the xerosere, the forest has been planted mainly in the *Violeto-Corynephoretum dunense* and the *Polypodieto-Empetretum.*

On Ameland and Schiermonnikoog, however, the *Festuceto-Galietum* covers large areas; in the xerosere, afforestation has been carried out mainly in this association, and further in the *Violeto-Corynephoretum* and in the *Salix repens-Thalictrum minus*-association.

The hygrosere, as far as it relates to our subject, is given in schemes II and III. Two schemes are given, since the oligotrophic hygrosere on Terschelling, where *Empetrum nigrum, Erica tetralix, Calluna vulgaris and Myrica gale* are important constituents, differs considerably from the less oligotrophic hygrosere on Ameland and Schiermonnikoog, where these species are less common (*Calluna*) or even rare (*Erica*) or absent (*Myrica*). The names of the communities in which afforestation has taken place (mostly after draining) have been printed in italics.

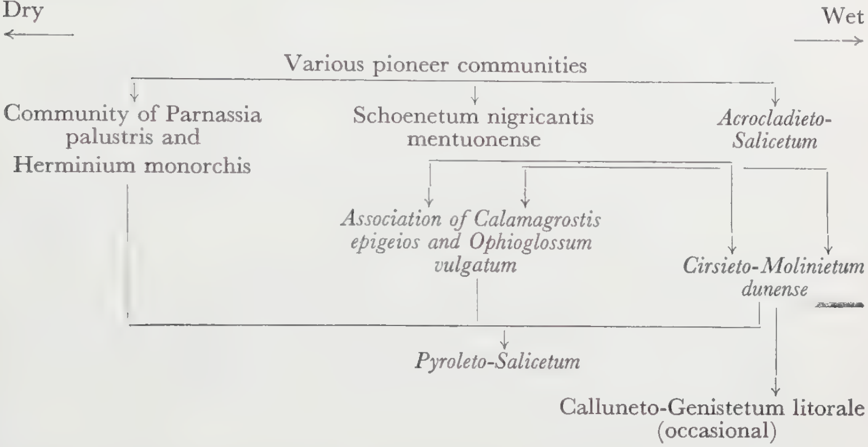
SCHEME II

The Hygrosere on the island of Terschelling


Dry
We
Various pioneer communities
Schoenetum nigricantis metuonense
Acrocladieto-Salicetum
Ass. of Calamagrostis epigeios and Ophioglossum vulgatum
Pyroleto-Salicetum
Empetro-Ericetum
Calluneto-Genistetum litoralis
Littorellion uniflorae
Caricetum trinervis-fuscae
Sociation of Oxycoccus macrocarpu
Sociation of Myrica gale
Betuleto-Salicetum, variant with Carex trinervis

SCHEME III

The Hydrosere on the islands of Ameland and (or) Schiermonnikoog


Dry
Wet
Various pioneer communities
Community of Parnassia palustris and Herminium monorchis
Schoenetum nigricantis mentuonense
Acrocladieto-Salicetum
Association of Calamagrostis epigeios and Ophioglossum vulgatum
Cirsieto-Molinietum dunense
Pyroleto-Salicetum
Calluneto-Genistetum litorale (occasional)

The xero- and hygrosere mostly alternate over short distances, because of the geomorphological situation.

The undergrowth of the pine plantations differs according to the depth of the water table. In the pure xerosere, they remain very poor in species. In the first decennium, there is either no undergrowth at all, or only the mosses *Hypnum cupressiforme*, *Dicranum scoparium* and *Pleurozium schreberi*. In some cases, mainly along woodland margins, certain phanerograms may survive, though sparsely and with reduced vitality, e.g. *Ammophila arenaria*, *Carex arenaria* and *Salix repens*. In the next decennia the moss cover becomes denser and some phanerogams may either return or spread secundarily, e.g. *Agrostis canina* var. *arida*, *Polypodium vulgare*, *Epipactis helleborine*, *Empetrum nigrum*, *Hieracium umbellatum* and *Veronica officinalis* besides those mentioned previously. As yet, no *Vaccinium* species are established, and *Listera cordata* has not been found in such dry pine forests.

Pine forests in the pure hygrosere do not exist, because of the above-mentioned sylvicultural reasons. However, considerable stretches of pine forest are found in an intermediate habitat, where species of both xero- and hygrosere occur, and which may be named "mesosere" (DEN HARTOG 1952). *Listera cordata* has been observed in this habitat only. Eight sample plot vegetation analyses (records) were made by us in this biotope and are combined in table 3. The records 2 and 3 have been made on the same locality, but in different years and by different investigators.

A ninth analysis for the Culbin Sands on the Scottish coast (see § 3) was made and this agrees quite well with the other records. This may be due:

(1) to the corresponding climate: the climate of Culbin Sands is known to be relatively mild and dry for Scottish conditions, the precipitation amounting to 61–67 cm per annum (OVINGTON,

1950). Terschelling with 72 cm has a rainfall which is not considerably higher;
(2) to the similar geological and geomorphological situation;
(3) to similar history: until 1921 the Culbin Sands were a desert where the dune sand was freely blowing until it was fixed by afforestation; in the same way, only two decennia before, the dune landscape of Terschelling constituted a rather bare desert until it was fixed by various techniques, e.g. afforestation, erosion control and the abolishment of dune pasturing;
(4) to the similar ages of the forests studied: 45 years in the Culbin Sands, 30–40 years on the islands;
(5) to the fact that the dominant tree is the same.

The most constant, characteristic differential species of this community is *Pseudoscleropodium purum;* it can be said, that it is useless to look for *Listera cordata* where this moss is absent. Therefore, the present community can be indicated as a "*Pinis nigra + sylvestris – Listera cordata – Pseudoscleropodium purum*-consociation".

Mr. S. SEGAL kindly informed us:
(1) that he observed, that, during the years 1950–1958, in the pine-forests on Terschelling the presence and dominance of *Pseudoscleropodium purum* increased;
(2) that this moss species does not at all play the same part in the Scandinavian pinewoods, where *Listera cordata* is constantly associated by *Hylocomium splendens* and less frequently also by *Ptilium crista castrensis* and *Pleurozium schreberi.* In our table 3, the combination of these three species (and also *Pseudoscleropodium purum*) with *Listera cordata* is represented in record nr. 3 only.

A certain resemblance between the forest habitat and that of the dwarf dune scrub is obvious. Therefore in table 3 we listed separately not only the species of the xero- and the hygrosere, but also those species which occur on the islands in dune scrub or have their optimal habitat on northern exposures (which in most cases bear also a dwarf scrub community). The remaining species have been separated into a xerosere group, a hygrosere group and a (very small) group of species indifferent in this respect; besides, the "differentials" of Culbin Sands are given as a special category. Among the latter are (1) taxa which are completely wanting on the islands, viz. *Deschampsia flexuosa*, *Frangula alnus*, *Betula pubescens* ssp. *odorata*, and *Pyrola secunda;* (2) *Galium hercynicum*, which is known on the islands from only one locality on Terschelling, far from the forests; (3) *Holcus mollis*, which occurs on the islands only in alder wood.

In order to obtain a numerical expression of the position of the records between the xero- and the hygrosere, we have calculated the group quotient X/H. 100. The total cover values of the group of xerosere and hygrosere species of each record (X and H) have been calculated by addition, the cover values being made according to SCHWICKERATH (see e.g. WESTHOFF, 1947). If the total cover value of the xerosere species is lower than that of the hygrosere species, the group quotient

TABLE III

Pine forest community on the Westfrisian islands and the northern Scottish dune coast as a habitat of Listera cordata. (Pinus nigra + sylvestris — Listera cordata — Pseudoscleropodium purum-consociation).

T = Terschelling, Neth.
A = Ameland, Neth.
S = Schiermonnikoog, Neth.
Cs = Culbin Sands, Scotland

W = West of the island
H = Hoorn
N = Nes
M = Mörzer Bruijns

Se = Segal
V = Vlieger
W = Westhoff
ep. = epiphyte

Number	1	2	3	4	5	6	7	8	9
Island or region	T	T	T	T	T	T	A	S	Cs
Locality	W	W	W	W	H	W	N	—	—
Author	W	Se	M, W	Se	W	W	V, W	W	M, W
Year ('19)	'53	'55	'57	'55	'55	'58	'51	'56	'56
Date	16–6	28–6	1–8	28–6	30–6	2–9	11–7	24–8	1–7
Tree layer, age in years	32	± 30	30	30	32	30	35	40	45
Tree layer, height in meters	11	8–10	8–10	8	8–9	8	8	10	15–20
Tree layer, degree of dominance in %	80	80	80	80	80	90	80	70	80
Shrub layer, height in m	1–2	0,5–2,5	1–3	0,5–3	1–4	0,3–1	3–4	—	—
Shrub layer, degree of dominance in %	20	25	40	30	30	20	( )	—	—
Herb layer, degree of dominance in %	30	30	<5	10	20	40	80	50	<1
Moss layer, degree of dominance in %	40	30–40	60	50	20	100	80	90	100
Surface studied, in square meters	200	100	90	100	150	200	100	100	100
Tree layer (cultivated, species introduced)									
Pinus nigra ssp. nigra	5.1	5.1	—	—	5.1	—	5.1	4.1	—
Pinus nigra ssp. laricio	—	—	5.1	5.1	—	—	—	—	5.1
Pinus sylvestris	—	—	—	—	—	5.1	—	—	—
Shrub layer (cultivated, species introduced)									
Sorbus aucuparia	1.1	1.1	1.1	+–1.1	+.1	+.1	—	—	—
Quercus robur	2.1	2.1	—	1.1	3.1	2.1	—	—	—
Acer pseudoplatanus	+.1	+.1	—	—	+.1	+.1	—	—	—
Fagus sylvatica	+.1	—	—	—	+.1	+.1	—	—	—
Prunus serotina	—	+.1	3.2–3	2.2	—	2.1–2	—	—	—
Picea sitchensis	+.1	—	—	—	—	—	—	—	—
Fraxinus excelsior	+.1	+.1	—	—	—	—	—	—	—
Ilex aquifolium	—	—	+.1	+.1	—	—	—	—	—
Shrub layer (spontaneous, native species)									
Myrica gale	+.1	+.1	—	—	—	—	—	—	—
Sambucus nigra	—	—	—	—	—	—	+.1	—	—

TABLE III *(Continued)*

Number	1	2	3	4	5	6	7	8	9
Herb layer and moss layer:									
I. *Neophytes* (woodland species)									
Listera cordata	2.1	1.1	1.1†	1.1–2	1.1–2	(+.2)	1.1	1.1–2	+.3
Goodyera repens	—	—	+.2	—	—	2.2	—	—	1.1
Linnaea borealis	—	—	—	—	—	3.4	—	—	—
Lycopodium annotinum	—	—	—	—	—	—	—	+.2	—
Ptilium crista-castrensis	—	—	(+.2)	+.2	—	—	—	—	—
Plagiothecium undulatum	—	—	+.2	—	—	—	—	—	—
Cantharellus aurantiacus	—	—	+.1	—	—	—	—	—	—
II. *Species, occurring on the islands in dune shrub or having their optimal habitat on northern exposures:*									
Dryopteris spinulosa	+.2	+.2	+.2	+.2	+.2	+.1	2.2	+.1	+.1
Polypodium vulgare	+.2	1.2	1.2	+.2	—	1.2	1.2	+.2	+.1
Pyrola rotundifolia	+.2	+.2	—	+.1	+.3	—	—	+.1	—
Pyrola minor	—	+.2	—	—	1.2–3	—	2.4	—	+.1
Rubus fruticosus	+.1	+.2	—	—	+.1	—	+.1	—	—
Dicranum scoparium	—	—	+.2	+.2	—	1.2	—	1.2	2.3
Eurhynchium stokesii	—	—	+.3	—	1.2	—	+.3	—	—
Lophocolea bidentata	—	+.2–3	2.3	2.3	ep.	1.3	—	2.3	+.2
Pleurozium schreberi	—	—	+.2	+.2	—	+.3	—	3.4	—
Salix repens	—	—	—	+.1	+.1	—	—	—	—
Epipactis helleborine	—	—	—	—	—	—	+.1	+.1	1.2
Plagiothecium denticulatum	—	+.3	+.3	—	—	—	—	—	—
Brachythecium rutabulum	—	—	—	—	+.2	—	+.2	—	+.2
Calluna vulgaris	—	—	+.2	—	—	—	—	—	—
Sambucus nigra, iuv.	—	—	—	—	—	—	—	+.1	—
Hippophae rhamnoides	—	—	—	—	—	—	—	+.1	—
Rosa canina, iuv.	—	—	—	—	—	—	—	+.1	—
Crataegus monogyna, iuv.	—	—	—	—	—	—	—	+.1	—
Dryopteris filix-mas	—	—	+.2	—	—	—	—	—	—
Lonicera periclymenum	—	—	—	—	1.2	—	—	—	—
Hylocomium splendens	—	—	—	+.2	—	—	—	—	—

Viola canina	—	—	+.1	+.1	—	—	2.2	+.2	—
Senecio jacobaea	—	—	—	—	—	—	+.1	+.1	+.1
Agrostis canina var. arida	—	+.1–2	2.2–3	2.2–3	—	2.1–2	1.2	—	—
Epilobium angustifolium	+.2	—	—	—	—	—	—	—	+.2
△AS Galium mollugo	—	—	—	—	—	—	+.2	+.1	—
△AS Asparagus officinalis	—	—	—	—	—	—	+.1	+.1	—
Ammophila arenaria	+.1°	—	—	—	—	—	—	—	—
Rumex acetosella	—	+.1	+.2	—	—	—	—	—	—
Galium verum	—	—	—	—	—	—	+.1	—	—
Linaria vulgaris	—	—	—	—	—	—	1.1	—	—
Viola tricolor var. stenochila	—	—	—	—	—	—	+.1	—	—
Stellaria media	—	+.2	—	—	—	—	—	+.1	—
△AS Thalictrum minus ssp. dunense	—	—	—	—	—	—	+.1	—	—
IV. *Species of the hygrosere of the dunes* (△AS: absent from Terschelling at all)									
Pseudoscleropodium purum	3.4	2–3.3	4.4	3.3	2.3	5.5	5.5	2.3	2.2
Calamagrostis epigeios	—	—	+.2	—	2.1–2	1.2	2.1	2.3	—
Lotus uliginosus	—	—	—	—	+.1	—	+.2	—	+.1
Cirsium palustre	—	—	—	—	+.1	—	+.1	+.2	—
Taraxacum sect. Vulgaria	—	—	—	—	+.1	—	+.1	+.1	—
Poa pratensis	—	—	—	—	+.2	—	1.1	+.1	—
Holcus lanatus	+.2	1.2	1.1–2	1.2	—	1.1–2	+.2	—	—
Luzula multiflora	—	+.2	1.2	+.1	+.1	+.1	—	—	—
Anthoxanthum odoratum	—	—	—	—	+.1	—	1.1	—	—
Galium palustre	—	—	—	—	(+)	—	+.2	—	—
Ranunculus repens	—	—	—	—	(+)	—	—	+.1	—
△AS Listera ovata	—	—	—	—	—	—	+.1	—	—
Juncus effusus	—	—	—	—	+.2	—	—	—	—
Hydrocotyle vulgaris	—	—	—	—	+.1	—	—	—	—
Orchis maculata	+.1	( )	—	( )	—	—	—	—	—
Potentilla erecta	+.1	+.1	—	—	—	—	—	—	—
Carex flacca	—	—	—	—	—	—	+.1	—	—
Cerastium holosteoides	—	—	—	—	—	—	1.1	—	—
Platanthera bifolia	—	—	—	—	—	+.1	—	—	—
Ranunculus acer	—	—	—	—	—	—	+.1	—	—
Sieglingia decumbens	—	—	—	—	—	—	+.2	—	—
V. *Species, indifferent re xero- or hygrosere*									
Hypochoeris radicata	+.1	—	+.1	—	+.1	+.1	+.1	—	+.1

TABLE III *(Continued)*

	Number	1	2	3	4	5	6	7	8	9
	Hypnum cupressiforme	—	—	2.2–3	2.3	—	1.3	—	3.3	4.4
	Peltigera canina	—	—	—	—	—	—	—	+.3	+.2
	Vicia angustifolia	—	—	+.2	—	(+)	—	—	—	—
	Pohlia nutans	—	—	+.2	—	—	—	—	—	—
VI.	*Species absent from the islands or only rare and local there ("differentials" of Culbin Sands)*									
	Deschampsia flexuosa	—	—	—	—	—	—	—	—	+.2
	Frangula alnus, iuv.	—	—	—	—	—	—	—	—	+.1
	Pyrola secunda	—	—	—	—	—	—	—	—	+.1
	Betula pubescens ssp. odorata	—	—	—	—	—	—	—	—	+.1
	Galium hercynicum	—	—	—	—	—	—	—	—	+.1
	Holcus mollis	—	—	—	—	—	—	—	—	+.2
VII.	*Seedlings of cultivated trees*									
	Sorbus aucuparia	+.1	+.1	1.1–2	1.1	—	+.1	—	+.1	—
	Quercus robur	+.1	+.1	+.1	+.1	—	+.1	—	—	—
	Prunus serotina	+.1	—	1.1	1.1–2	—	+.1	—	—	—
	Viburnum opulus	+.1	—	(+)	—	—	—	—	—	—
	Pinus nigra ssp. laricio	—	—	r	+.1	—	—	—	—	—
	Picea sitchensis	—	—	r	—	—	—	—	—	—
	Quercus borealis	—	—	—	—	+.1	+.1	—	—	—
	Crataegus monogyna	—	—	—	+.1	—	—	—	—	—
	Group quotient X/H. 100	75	64	64	71	25	70	75	70	60

must be < 100. Indeed, in our records it varies from 25 to 75 (see table 3), thus indicating (1) that all records belong to the hygrosere; (2) that, nevertheless, the xerosere species always remain of importance, so that it might be better to bring the *Pinus nigra + sylvestris – Listera cordata – Pseudoscleropodium purum*-consociation to the "mesosere".

It is interesting, that the populations of *Listera cordata* on the islands are so large; in table 3, the abundance figure 2 refers to thousands of individuals, figure 1 to many hundreds of them, on sample surfaces of circa 100 m^2. For the Ameland locality, WEIJER (1949) observed ca. 10,000 individuals on 20 m^2. SUMMERHAYES (1951) states, that the number of individuals of *Listera cordata* is rather small in most cases, and that such large populations arise only where the habitat is optimal. It is surprising, that such young and artificial pine stands with only a thin fermentation cover on sterile dune sand offer such optimal conditions for this particular species.

Comparing the difference in the dominant tree species with any difference in undergrowth vegetation, it appears from table 3, that in one record (no. 6) *Pinus sylvestris* is the dominant tree. This is exceptional: the record represents one of the very few spots on the island of Terschelling where *Pinus sylvestris* has been planted instead of *Pinus nigra*. This record is also the only locality of *Linnaea borealis* known on Terschelling; whether this correlation is accidental or real, cannot be concluded on the base of a single record. As to the subspecies of *Pinus nigra*, table 3 shows that there is no obvious correlation between the difference in the dominant tree subspecies and any of the differences in vegetation.

Comparing the *Pinus nigra + sylvestris – Listera cordata – Pseudoscleropodium purum*-consociation (table 3) with the *Pineto-Vaccinietum myrtilli atlanticum* of Scotland (table 2 and context), we see that these communities have 17 species in common. Five of them are neophytes in the dune sociation: *Listera cordata*, *Goodyera repens*, *Linnaea borealis*, *Plagiothecium undulatum*, *Ptilium crista-castrensis*. Except for *Linnaea*, these are all "euchorous" species (WESTHOFF, 1947), i.e. species with a large dissemination capacity, which in this case is due to very small diaspores enabling the plants to establish themselves as soon as the habitat becomes favourable. *Linnaea borealis* is supposed to be epizcöchorous, viz. to be transported by migratory birds (GIGER 1913, BEYERINCK 1929b); in this case it would be an euchorous species too. Among the other species which both communities have in common, 8 belong to the group of species occurring on the islands in dune scrub or having their optimal habitat on northern exposures; they are, in sequence of degrees of presence in table 3: *Dryopteris spinulosa*, *Pyrola rotundifolia*, *Pyrola minor*, *Dicranum scoparium*, *Pleurozium schreberi*, *Calluna vulgaris*, *Hylocomium splendens*, *Sorbus aucuparia* (the last one in table 3 probably subspontaneous). These species, too, are euchorous. Of the four remaining species occurring in both communities, two are from the xerosere (*Veronica officinalis* and *Rumex acetosella*), one from the hygrosere (*Potentilla erecta*) and one, *Agrostis canina*, which in its main from (var. *canina*?) is hygrophilous, but in its var. *arida* not so.

The last species worth mentioning is *Dryopteris linnaeana.* It belongs to the first group, that of neophytes in the dune sociation, but it has not been considered above, as it is absent from both our tables 2 and 3. It does occur, however, in the Scotch pinewood, and it was discovered, for the first time on the Westfrisian islands, by Mr. S. Segal in an artificial pine forest on the island of Terschelling in the year 1955.

Finally we may ask what probability there is for a future development of the pine-consociation on the islands, from the present "nascent association", to a well-developed association of the sub-alliance *Piceion septentrionale.* This is mainly a question of accessibility. As to the dominant *Vaccinium* species, experience on the Dutch mainland has taught us that they do not establish themselves in artificial pinewoods in the first generation under 25 years of age (Westhoff, 1957). Assuming that it would be allowed to apply this to the islands, the establishment of these species might be expected now from an edaphic point of view. *Vaccinium myrtillus* however is completely absent from the islands as yet. *Vaccinium vitis-idaea* occurs in the dune scrub of Terschelling as a neophyte in 2 localities, probably brought by migratory birds; its establishment in the pine forest is possible, but it has been found neither on Ameland nor on Schiermonnikoog. The same is true for *Arctostaphylos uva-ursi,* a recent neophyte on Terschelling, and known there from 3 localities in open dune heath; for *Juniperus communis,* also known from Terschelling dune scrub; and for *Blechnum spicant,* a recent neophyte in one locality in dune scrub on Terschelling. *Rhytidiadelphus loreus* and *R. triquetrus* occur on Terschelling, especially in the *Polypodieto-Empetretum* on northern slopes, and we do not see any reason why they should not be able to establish themselves in the pine forest. *Sphagnum girgensohnii* and *S. quinquefarium* are montane species, not likely to be expected in a lowland dune area. *Trientalis europaea* occurs on Terschelling in alder wood where the soil is not covered with a humus layer comparable to that of the pine forests. In 1958, however, it has been observed on Terschelling also in rather open, low dune shrub in the mesosere; in a similar habitat it had been observed on the island of Vlieland as early as 1928 (de Vries, 1950), on which locality, however, it did not maintain itself. We do not expect a migration of *Trientalis europaea* into the Terschelling pineforests in the near future.

Summarizing, we may expect a further development of the pine forest of Terschelling into a well-defined association of the *Piceion septentrionale.* This is mainly due to the exceptionally low lime content of the Terschelling dune sand, favouring the establishment of species of the boreal coniferous woodland formation. Such a development is less probable on Ameland and Schiermonnikoog.

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REFERENCES

ANON. 1953. Culbin Forest. Leaflet, Britain's Forests, Forestry Commission.

AICHINGER, E. 1949. Grundzüge der Forstlichen Vegetationskunde.

ASCHERSON, P. & P. GRAEBNER. 1905–1907. Synopsis der Mitteleuropäischen Flora. III.

BARKMAN, J. J. 1951. Impressions of the North Swedish Forest Excursion. Vegetatio III, **3**: 175–182.

———. 1958 (a). On the ecology of cryptogamic epiphytes.

———. 1958 (b). Phytosociology and Ecology of cryptogamic epiphytes.

———. 1958 c). Nieuwe vindplaatsen van Lycopodium annotinum, L. selago en Goodyera repens en hun standplaats. Corr. blad Floristiek en Vegetatie-onderzoek Ned. 11, 112–116.

BEYERINCK, W. 1929 (a). De flora van het "Drentsch-District" II. De Levende Natuur **33**: 343–347.

———; 1929 (b). Linnaea borealis L. De Levende Natuur **34**: 113–123.

———. 1936. Aantekeningen over het noorden van Finsch Lapland. Tijdschrift Kon. Ned. Aardrijksk. Gen.: 204–230.

BOERBOOM, J. H. A. 1957. Les pelouses sèches des dunes de la côte néerlandaise. Acta bot. neerl. **6**: 642–680.

BOODT, P. 1934. De bebossing op de Noordzee-eilanden. Ned. Boschbouw-Tijdschrift **7**: 177–195, 217–226, 286–306, 329–337, 369–377, 409–419, 437–469.

BRAUN-BLANQUET, J. & W. C. DE LEEUW. 1936. Vegetationsskizze von Ameland. Ned. Kruidk. Archief **46**: 359–393.

BRAUN-BLANQUET, J., G. SISSINGH & J. VLIEGER. 1939. Prodromus der Pflanzengesellschaften. Fasz. 6, Klasse der Vaccinio-Piceetea.

BUCHENAU, F. 1894. Flora der nordwestdeutschen Tiefebene.

———. 1936. Flora von Bremen, Oldenburg, Ostfriesland und der ostfriesischen Inseln. 10th ed.

CHRISTIANSEN, W. 1953. Neue kritische Flora von Schleswig-Holstein.

CLAPHAM, A. R., T. G. TUTIN & E. F. WARBURG. 1952. Flora of the British Isles.

COMMELIN, J. 1683. Catalogus Plantarum Indigenarum Hollandiae.

DIEREN, J. W. VAN. 1934. Organogene Dünenbildung, eine geomorphologische Analyse der westfriesischen Insel Terschelling mit pflanzensoziologischen Methoden.

FOURNIER. P. 1946. Les quatre flores de la France.

GIGER, E. 1913. Linnaea borealis, eine monographische Studie.

GORTER, D. DE. 1781. Flora VII provinciarum Belgii foederati indigena.

GROSSER, K. H. 1955. Fichte und Tanne im Waldbild der Lausitz. In: W. R. Müller-Stoll, Die Pflanzenwelt Brandenburgs: 56–64.

HARTOG, C. DEN. 1952. Sociologische waarnemingen op Schiermonnikoog. Kruipnieuws **14**: 2, 2–24.

HEGI, G. W. D. (1909). Illustrierte Flora von Mitteleuropa II.

HERMANN. 1956. Flora von Nord- und Mitteleuropa.

Hoogenraad, H. R. 1951. Biogeografie. In: G. J. A. Mulder, Handboek d. geogr. v. Ned., **2**: 1–129.

Hultén, E. 1950. Atlas of the distribution of vascular plants in N.W.-Europe.

Kujala, V. 1929. Untersuchungen über Waldtypen in Petsamo und in angrenzenden Teilen von Inari-Lappland. Comm. Inst. quaest. forest. Finlandiae, 13.

Lawalrée, A. & C. Vandenberghen. 1946. Note sur quelques phanérogames de la flore Belge. Bull. de la Soc. roy. botan. de Belg., **78**: 100–105.

Macvicar, S. M. 1912. The Student's Handbook of British Hepatics.

Metcalfe, G. 1950. The mountain Callunetum. Journal of Ecology **38**: 46-74.

Meyer, W. & J. van Dieken. 1947. Pflanzenbestimmungsbuch für die Landschaften Osnabrück, Oldenburg-Ostfriesland und ihre Inseln, Band **1**.

Mörzer Bruijns, M. F. & V. Westhoff. 1951. The Netherlands as an environment for insect life.

Nordhagen, R. 1939–1940. Studien über die maritime Vegetation Norwegens I. Die Pflanzengesellschaften der Tangwälle. Bergens Mus. Årb. natv. r. 2.

Oberdorfer, E. 1949. Pflanzensoziologische Exkursionsflora für Südwest-deutschland und die angrenzenden Gebiete.

————. 1957. Süddeutsche Pflanzengesellschaften.

Oudemans, C. A. J. A. 1874. De Flora van Nederland, **3**.

Ovington, J. D. 1950. The afforestation of the Culbin Sands. Journ. of Ecol. **38**: 303–319.

Palmgren, A. 1922. Zur Kenntnis des Florencharakters des Nadelwaldes I. Acta Forestalia Fennica **22** (2): 1–115.

Plantenkaartjes van Nederland. 1937. Nederl. Kruidk. Archief **47**: 196–227.

Poore, M. E. D. 1955. Phytosociological methods in ecological investigations. Journal of Ecology, **43**: 226–269, 606–651.

Praeger, R. Ll. 1934. The botanist in Ireland.

Prodromus Florae Batavae ed. altera. 1902. I, 2. 1916, I, 4.

Raunkiaer, C. 1942. Dansk Ekskursions-flora.

Schütt, B. 1936. Die Pflanzengemeinschaften. In: Buchenau Flora von Bremen (etc.).

Sjörs, H. 1949. Några växter funna huvudsakligen år 1948. Botaniska Notiser: 95–103.

Steffen, H. 1931. Vegetationskunde von Ostpreussen.

Summerhayes, V. S. 1951. Wild orchids of Britain.

Tansley, A. G. 1949. The British Islands and their Vegetation.

Vries, V. de. 1950. Vlieland, Landschap en Plantengroei.

Webb, D. A. 1943. An Irish Flora.

Westhoff, V. 1943. Plantensociologisch onderzoek, in het bijzonder op de Waddeneilanden. Hand. v. h. Ned. Nat. en Geneesk. Congres.

————. 1947. The vegetation of dunes and salt marshes of the Dutch islands of Terschelling, Vlieland and Texel.

————. 1952. Gezelschappen met houtige gewassen in de duinen en langs de binnenduinrand (summary: Plant communities with woody species found in the Dutch dune area and its inner border). Jaarb. Ned. Dendrolog. Ver.: 9–49.

————. 1954 (a). Landschap en Plantengroei van Schiermonnikoog. Natuur en Techniek, **22**: 188–192, 240–245.

————. 1954 (b). Die Vegetationskartierung in den Niederlanden. Angewandte Pflanzensoziologie, Festschrift E. Aichinger 1223–1231.

————. 1955. Vegetatie-kartering. T.N.O.-nieuws, **107**: 61–67.

————. 1957. Een gedetailleerde vegetatiekartering van een deel van het bosgebied van Middachten (summary: A detailed vegetation map of a part of the woodland of Middachten in the Netherlands). Publ. L.E.B. fonds, Belmontia II Ecology: **2**: 1–58.

Weijer, J. 1949. Listera cordata in Nederland teruggevonden. De Levende Natuur **52**: 200.

W(ilcke), J. 1958. Het Linnaeusklokje op Terschelling. De Levende Natuur **61**: 166.

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SOME NOTES ON SKALLINGENS SALT MARSH VEGETATION AND ITS HABITAT

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1. Introduction

From 1–7 July 1956 an excursion was organized through Schleswig and Jutland by the International Society for Plant Geography and Ecology. The objects were salt marshes and dunes along the coasts of the Wadden Sea and the North Sea. During this excursion Dr. J. Iversen invited the author kindly to stay some days (5–8 July) at Skalling-Laboratory, situated in the northern part of the Danish peninsula Skallingen near the village Ho. The author is greatly indebted to Dr. Iversen for his kind invitation, which enabled him to carry out the present work.

The Skalling Peninsula — about 3 × 10 km large — forms the northern barrier of the Danish Wadden Sea, which ends in the Ho Bugt. The narrow but deep channel Graadyb separates it from the isle of Fanø. Skallingen is one of the most northern regions with salt marshes on the west coast of Denmark and therefore it is of major importance for the study of the Westeuropean halophytic biocenoses.

On the side of the North Sea the peninsula consists of dunes with beaches. These dunes form the southern continuation of the chains along the west coast of Jutland. Behind the dunes a sandy and hilly landscape is found, for the greater part situated at an altitude fairly high above MHW-level. The more clayey salt marshes are found further on to the east along the Wadden Sea, largely overgrown with a closed vegetation which is flooded by spring-tides and storm floods.

It was not possible to study the whole salt marshes in the few days available. Therefore a rather small region was chosen, which, apparently, never had been grazen by cattle. This region forms a strip going from the Wadden Sea to the west overlapping both clayey and sandy soils (Fig. 1).

2. Environment and geomorphological development

The foundation on which the marshes have been formed is a sand flat of higher level than normal tidal flats (Jakobsen, 1952/53). Through several gaps in the dunes the sea deposited a great deal of sand behind the coastline. In the beginning of this century, however, the gaps were closed by dams and since the salt marshes and their vegetation have developed. The first marshes were formed as small islands along the Wadden Sea. About 1931–1934, when Iversen (1936) investigated the vegetation of Skallingen, the area was divided

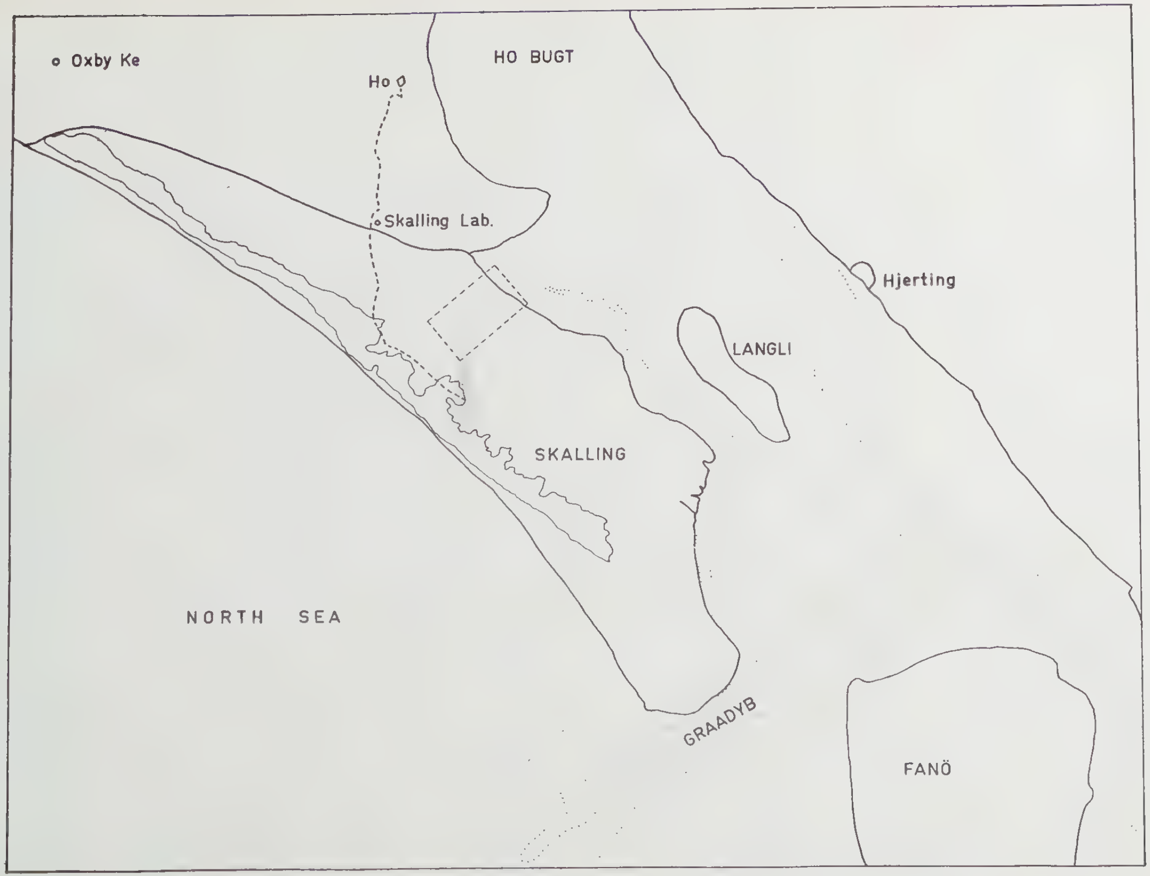

Fig. 1. Sketch map of Skallingen. (scale 1: 120.000). The area studied has been marked with a rectangle.

into so-called "outer salt marshes" situated on the Wadden Sea coast, and "inner salt marshes" near the dunes, which were separated by "a large sandplain nearly barren except for scattered *Salicornia*, often submerged by salt water for considerable periods" (Iversen, 1952/53). Nowadays the sandplain is silted up entirely and the outer and inner marshes overlap. This phenomenon of sedimentation of silt after closing gaps in the range of dunes is not restricted to Skallingen. It is observed, too, on the Dutch isles of Texel and Terschelling (Westhoff, 1947 manuscript).

On Skallingens salt marshes sedimentation from the Wadden Sea did not take place over the whole area. The inner marshes have only occasionly been silted up on a few localities, as a result of the fairly high elevation above MHW-level. This circumstance combined with the effect of a small number of tidal creeks and of the large distance to the sea results in inundations by storm floods only. In those circumstances the possibilities for sedimentation of silt are limited. For this reason the greater part of the area will have obtained its present condition, during the period that gaps in the dune ranges still existed. The outer marshes are younger and have been silted up recently. Locally, some sandhills emerge out of the clayey soil. They are probably high parts of the underlying sand flat. The formation of many tidal creeks with their banks and basins between them results in a landscape characteristic for such salt marshes. It may be called a bank-and-basin-landscape (Fig. 2). The tidal creeks are not so deep as those in the southwestern part of the Netherlands. Doubtless this phenomenon is related to the difference in tide-level (near Skallingen average about 1.35 m, in the S.W.-Netherlands 3.— till 4.50 m).

Except for the mud flats along the Wadden Sea the outer marshes are silted up to a height exceeding average high tide level. The rate of sedimentation was about 3,6 mm p.a. in the years 1931–1933 as stated by Nielsen (1935), but according to Jakobsen (1952/53) the real accretion was only some 2 mm due to settling in young deposits. However, the above mentioned authors have made no distinction

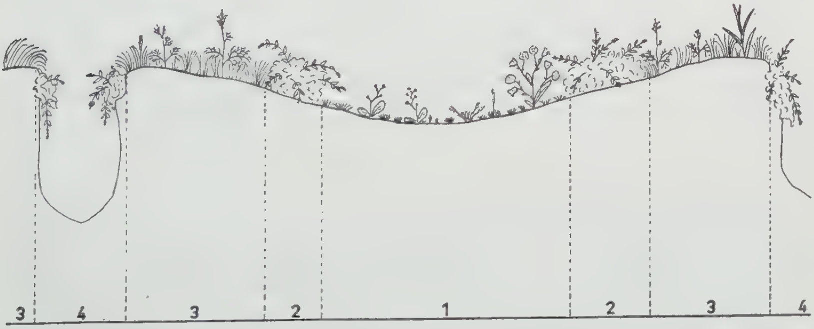

Fig. 2. Cross-section of the bank-and-basin-landscape with vegetation zones. 1 = *Puccinellietum maritimae;* 2 = *Halimionetum portulacoidis;* 3 = *Artemisietum maritimae;* 4 = Creeks with individuals of *Halimione portulacoides* on the walls along the inside of the banks.

between the difference of accretion in basins and that on banks a result of the difference in distance from the water-supplying creeks, for according to Verhoeven (1954) accretion on the banks is generally larger than in the basins, and, moreover, deposits were found to settle on banks to a lower degree.

On account of the sandy character of the inner marshes and their less frequent floods the soil moisture and its salt content are on an average lower compared with the outer marshes. The floristic composition and structure of the vegetation presents evident consequences of these differences in soil and water conditions.

The lime content of the soil is very low. According to Sanders and Verhoeven (1956) it decreases regularly on the salt marshes from Bretagne till Denmark. The soil of Skallingen still contains some lime, in contrast to some soils along the coast near Skaerbaek and Ribe which contain practically no lime (Verhoeven, verbal communication). According to Verhoeven, in 8 samples the content varies from 0,36 till 1,46 % $CaCO_3$ with a variation from 0 till 32,5 % silt $< 16\ \mu$.

Probably this difference between Skallingen and the above mentioned Danish salt marshes is due to a complex of factors of which the following may be important: (1) the origin and age of sedimentation materials; (2) a difference in sedimentation velocity which may be directly proportional to the lime content; (3) locally, mixing of seawater with the acid, or at least less calcareous, water of small rivers (see also the view of De Smet, 1954) or (4) perhaps difference in withdrawal of $CaCO_3$ from the sediments as an additional effect of oxydation of iron sulphide (Van der Spek, 1952) and of oxydation and hydrolization of iron compounds (Rivière, 1942). It is uncertain which factor prevails, the first two being generally perhaps the most common as a cause of local differences. On Skallingen the rather high sedimentation rate might be the primary cause of the relative high lime content.

Spartina townsendii promoting sedimentation along the European coasts, has not acted such a part here. In 1931 and 1932 the species was planted a.o. on three places along the Ho Bugt (Jørgensen, 1934). According to Iversen (verbal communication) in 1940 it has been disseminated on Skallingen too, but up to now it has not much superseded the original vegetation. Probably the sandy character of the mud flats and the rather cold climate in comparison with S.-England, France and the Netherlands does not promote its extension.

3. The vegetation

Describing the vegetation of the ungrazed strip a distinction has been made between the former outer and inner marshes. Transitions between those habitats are left out of consideration. The floristic composition and structure of the vegetation has been analysed with the method of Braun-Blanquet (1951). The sample plot analyses (Becking, 1957) — Fr.: relevés, Ge.: Aufnahmen — have been assembled in the Tables I and II. In order to ensure as objective a survey as possible most analyses have been taken in transects perpendicular to the contour lines in the landscape. From low to high the transects consist of the following sample plot analyses:

Outer marshes
56022–56023–56024–56025
56027–56028–56029
56030–56031–56032–56033
56034–56035
56037–56038–56039
56045–56044
56046–56047–56048
56055–56054

Inner marshes
56057–56058–56059–56060–56061
56063–56064–56065–56066–56067–56068
56069–56070–56071–56072–56073
56075–56076–56078–56079–56080
56082–56081
56084–56085
56086–56087

3.1 *The outer salt marshes*

On the mud flats along the Wadden Sea *Zostera nana* grows locally (*Zosteretum nanae* Harmsen 1936). The mud flats are mostly bare, but *Spartina townsendii* establishes itself gradually. Near the closed vegetation of the higher marshes the flats are overgrown with a vegetation almost entirely consisting of *Salicornia europaea* scattered with clumps of *Spartina townsendii* (*Salicornietum europaeae* (Warming 1906) Hocquette 1927, see Table I). The abundance of the *Salicornia*-individuals was not large, but it increased on the higher parts being the largest in the transition to the next association, *Puccinellietum maritimae* (Warming 1890) Braun-Blanquet et De Leeuw 1936. However, vitality decreased in this association.

As a result of the sod-forming properties of *Puccinellia maritima* the transition from *Salicornietum europaeae* to *Puccinellietum maritimae* is rather distinct. The latter association appears at first in an initial phase, which may be distinguished from the optimal one by a more open turf (cover 20–40 % in contrast with 40–80 % in the optimal phase) and the lower frequency of individuals of *Halimione portulacoides* with reduced vitality. Moreover, *Spartina townsendii* occurs only in the initial phase up to now. The initial phase is found mainly along the mud flats, the optimal one in the basins between the banks of the tidal creeks. Although the abundance of *Salicornia europaea* in this association is rather large, vitality is evidently reduced. According to the analyses *Aster tripolium* is strictly confined to the *Puccinellietum maritimae* (compare also Table II). Therefore it might be considered as a local faithful species of the association.

The next association, *Halimionetum portulacoidis* (Chapman 1934) Des Abbayes et Corillion 1949, finds its habitat on the slopes of the banks, in the highly silted basins and, fragmentary, along the insides of the banks on the creek walls. It often includes *Limonium vulgare* in large quantities and, when it is not highly developed, *Plantago maritima var. dentata* Bl. et Fing. In the upper part *Artemisia maritima* appears locally, sometimes in large quantities (analyse 56051), perhaps due to favourable circumstances influencing the competition between *Artemisia maritima* on the one side and *Halimione portulacoides* and *Festuca rubra* on the other side. Other species such as *Aster tripolium*, *Triglochin*

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Vegetation of th

		Salicornietum europaeae					
Sample plot analyse nr.	56027	56026	56019	56030	56028	56018	56062
Surface in m²	4×5	8×10	8×50	25×30	5×15	15×30	4
Cover in %	20	1	1	1	1	1	1
Faithful taxa of the associations and sociation							
Salicornia europaea	+.1	1.1	1.1	1.1	1.1	1.1	2.1
Puccinellia maritima	—	—	—	—	—	—	+.1
Aster tripolium	—	—	—	—	—	—	—
Halimione portulacoides	—	—	—	—	—	—	—
Artemisia maritima	—	—	—	—	—	—	—
Agropyron litorale	—	—	—	—	—	—	—
Faithful taxa of the Puccinellion maritimae							
Spartina townsendii	2.5	+.1	+.2–3	1.2–3	+.1–2	1.1–3	—
Suaeda maritima	—	—	—	—	—	+.1	—
Spergularia marginata	—	—	—	—	—	—	—
Faithful taxa of the Puccinellion maritimae and Armerion maritimae together							
Triglochin maritimum	—	—	—	—	—	—	—
Limonium vulgare	—	—	—	—	—	—	—
Plantago maritima typicum and var. dentata	—	—	—	—	—	—	—
Festuca rubra f. litoralis	—	—	—	—	—	—	—

arshes of Skallingen

	nsition	Puccinellietum maritimae										
		initial phase						optimal phase				
	56031	56034	56022	56021	56023	56032	56036	56024	56033	56025	56037	56035
	8 × 20	3 × 12	5 × 10	5 × 12	6 × 20	5 × 10	8 × 10	5 × 10	5 × 15	10 × 20	12 × 20	4 × 12
	3	20	25	25	25	40	25	40	65	60	70	80
	2.5	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	1.1	2.1
2	1.1–2	2.4	2–3.5	2–3.5	2–3.5	3.5	2.5	3.5	3.4	4.5	4.5	3.3
	—	+.1	+.1	1.1–2	1.1–2	1.1–2	+.1	1.1–2	+.1–2	1.1–2	1.1–2	1.1–2
	—	+.1°	+.1°	+.1°	+.1	+.1°	+.1–2	1.1–2	2.1–3	2.1–3	2.2–3	2–3.2–3
	—	—	—	—	—	—	—	—	—	—	—	—
	—	—	—	—	—	—	—	—	—	—	—	—
3	—	+.1–2	1.1–2	1.2–3	+.1–2	1.2	+.2	—	+.2	—	—	—
	+.1	2.1	1.1	1.1	1–2.1	2.1	1.1	1.1	1–2.1	1.1	2.1	1.1
	—	—	—	—	—	+.1	—	—	—	—	—	+.1
	—	—	—	+.2	1.2–3	1–2.2	1–2.2	+.1–3	+.2	+.1–2	+.2	1.2
2	+.2	—	—	+.1	+.2	1.2	1–2.2	+.1–2	+.2	+.1–2	+.2	1–2.2–3
	—	—	—	—	—	—	—	—	—	—	—	+.2
	—	—	—	—	—	—	—	—	—	—	—	—

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Vegetation of the

	Transition		Halimion		
			optimal phase		
Sample plot analyse nr.	56053	56055	56045	56038	56050
Surface in m²	4×15	4×6	5×6	3×20	3×7
Cover in %	90	90	80	85	85
Faithful taxa of the associations and sociation					
Salicornia europaea	+.1°	+.1°	+.1°	+.1°	+.1°
Puccinellia maritima	2.1–2	2.2	2.2	+.2	+.1–2
Aster tripolium	+.1	+.1	—	+.1–2	—
Halimione portulacoides	2–3.2–3	3.2–3	4.3	5.5	4.3
Artemisia maritima	—	—	—	—	+.1
Agropyron litorale	—	—	—	—	—
Faithful taxa of the Puccinellion maritimae					
Spartina townsendii	—	—	—	—	—
Suaeda maritima	1.1	+.1	+.1	—	+.1°
Spergularia marginata	—	+.1	—	—	—
Faithful taxa of the Puccinellion maritimae and Armerion maritimae together					
Triglochin maritimum	+.2	—	+.2	+.2	—
Limonium vulgare	3.2–3	3.3	3.2–3	+.2	3.2
Plantago maritima typicum and var. dentata	2–3.2	2–3.2	1.2	1.2	2.2
Festuca rubra f. litoralis	—	—	—	—	—

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arshes of Skallingen

	acoidis		Artemisietum maritimae								Sociation with Agropyron litorale
	inal phase with Artemisia		initial phase		optimal phase						
2	56051	56049	56054	56046	56039	56047	56042	56040	56043	56048	56041
)	3×5	5×6	3×10	5×15	8×12	6×20	6×30	3×8	3×5	8×15	4×6
	100	90	100	>95	100	100	100	100	100	100	100
	+.1°	—	—	+.1°	+.1	—	—	–	—	—	·
2	+.1-2	1.2	1.2-3	—	·	—	—	—	—	—	—
	—	—	—	—	—	—	—	—	—	—	—
	4.4	5.5	3.3	3–4.2–3	1–2.2–3	1.1–3	+.1–3	+.1–2	+.2	+.1°	—
	3.5	1–2.1	2.1–2	1–2.1	2.1	1.1	1.1–2	+–1.1	3.5	1.1	+.1
	—	—	—	—	—	—	—	—	—	—	5.5
	—	—	—	–	·	—	—	–	—	—	—
	—	—	—	—	—	—	—	—	—	—	—
	—	—	—	—	—	—	—	—	—	—	—
	—	—	—	–	—		+.2	—	—	—	—
-2	1–2.2	2.2	2.1–2	2.2–3	1.1–2	2.1–2	1–2.2	+–1.1–2	2.4	2.1–2	—
	1.2	+–1.2	+.2	1.2	+.1	+.2	+.2	—	+.2	+.1	—
	—	1.2	4.4	4.4	5.5	5.5	5.5	5.5	4.5	5.5	+.2

TA

Vegetation of the

	Salicornietum europaeae			
Sample plot analyse nr.	56062	56063	56056	56
Surface in m²	4	5 × 15	2 × 3	4
Cover in %	1	< 1	35	
Faithful taxa of the associations				
Salicornia europaea	2.1	1.1	2.1	
Puccinellia maritima	+.1	+.1	3.5	
Aster tripolium	—	—	+.1	+
Juncus gerardi	—	—	—	
Sagina maritima	—	—	—	
Plantago maritima var. leptophylla	—	—		
Faithful taxa of the Puccinellion maritimae				
Halimione portulacoides	—	—	+.1	
Artemisia maritima	—	—	—	
Suaeda maritima	—	+.1	1.1	
Spergularia marginata	—	—	—	—
Faithful taxa of the Armerion maritimae				
Armeria maritima	—	—	—	
Parapholis strigosa	—	—	—	
Glaux maritima	—	—	—	
Carex extensa	—	—	—	
Euphrasia litoralis	—	—	—	
Faithful taxa of the Puccinellion maritimae and Armerion maritimae together				
Triglochin maritimum	—	—	+.1	
Limonium vulgare	—	—	+.1	+
Plantago maritima typicum and var. dentata	—	—	—	
Festuca rubra f. litoralis	—	—	—	
Other taxa				
Agrostis stolonifera var. stricta	—	—	—	
Phragmites communis	—	—	—	
Bryum sp.	—	—	—	
Dianthus deltoides	—	—	—	
Juncus anceps	—	—	—	
Lyngbya digueti Gom.	—	—	—	
Elymus arenarius	—	—	—	
Poa annua	—	—	—	
Poa pratensis	—	—	—	
Plantago coronopus	—	—	—	
Sagina procumbens	—	—	—	
Sedum acre	—	—	—	
Empetrum nigrum	—	—	—	
Sonchus arvensis	—	—	—	
Leontodon autumnalis	—	—	—	

arshes of Skallingen

Puccinellietum maritimae										
therophytes				phase with Limonium vulgare and Plantago maritima						
56075	56069	56058	56083	56076	56065	56070	56077	56066	56059	56060
4×6	3×5	10×20	2×4	3×5	3×8	3×5	2×8	5×10	8×10	6×12
70	60	55	90	70	60	75	40	70	25	65
1.1	2.1	2.1°	+.1	1.1	2.1	1.1	2.1	+.1	2.1°	+.1°
4.5	4.5	4.5	5.5	3.5	3–4.5	3.5	2.2–3	3.5	2.2–3	2.2
+.1	+.1	1.1	2.1–2	1–2.1	1.1	2.1–2	1.1	2.1	1.1	1.1
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
+.1	+.1	+.1	+.1	+–1.1	1.1	1–2.1	+.1°	1.1	+.1	1.1–2
—	—	—	—	—	—	—	—	—	—	+.1
2.1	2.1	+.1°	+.1	+.1	+.1	+.1	+.1	—	+.1	+.1°
—	+.1	1.1	1.1	+.1	1.1	+.1	—	+.1	1.1	1.1
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	+.1	—	+.1	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
+.2	+.2	+.2	+–1.1–2	+–1.1	+–1.2	+.2	2.2	+.2	+.2	+.1
—	+.1–2	1.1–2	+.1	2–3.2	2.1–2	2–3.2	1–2.2	2–3.2	2.2	2–3.2
—	+.2	—	+–1.2	+.1–2	+.1–2	2.1–2	1–2.1–2	2.1–2	2.2	3.2
—	—	—	—	—	—	—	—	—	+.2	+.2
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
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—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—

Vegetation of th

	Ju				
Sample plot analyse nr.	56061	56071	56078	56067	
Surface in m²	3 × 8	2 × 10	3 × 8	2 × 10	
Cover in %	100	100	100	100	
Faithful taxa of the associations					
Salicornia europaea	—	—	—	—	
Puccinellia maritima	—	—	—	—	
Aster tripolium	—	—	+.1	—	
Juncus gerardi	+.1–2	+.1–2	1.2	1.1–2	1-
Sagina maritima	—	—	—	—	
Plantago maritima var. leptophylla	—	—		—	
Faithful taxa of the Puccinellion maritimae					
Halimione portulacoides	+.1	+.1°	—	+.1°	
Artemisia maritima	+.1	—	—	—	
Suaeda maritima	—	—	—	—	
Spergularia marginata	—	—	—	—	
Faithful taxa of the Armerion maritimae					
Armeria maritima	+.1–2	+.1	+.1	+.1–2	
Parapholis strigosa	—	—	—	—	
Glaux maritima	—	—	—	—	
Carex extensa	—	+.1	+.1	+.1	
Euphrasia litoralis	—	—	—	—	
Faithful taxa of the Puccinellion maritimae and Armerion maritimae together					
Triglochin maritimum	+.1	+.1	+–1.1–2	+.1	
Limonium vulgare	2.1–2	1–2.1–2	+–1.1	1.1	
Plantago maritima typicum and var. dentata	+–1.1–2	1.1–2	+.1	+–1.1	+
Festuca rubra f. litoralis	5.5	5.5	5.5	5.5	
Other taxa					
Agrostis stolonifera var. stricta	—	—	—	+.1	
Phragmites communis	—	—	—	—	
Bryum sp.	—	—	—	—	
Dianthus deltoides	—	—	—	—	
Juncus anceps	—	—	—	—	
Lyngbya digueti Gom.	—	—	—	—	
Elymus arenarius	—	—	—	—	
Poa annua	—	—	—	—	
Poa pratensis	—	—	—	—	
Plantago coronopus	—	—	—	—	
Sagina procumbens	—	—	—	—	
Sedum acre	—	—	—	—	
Empetrum nigrum	—	—	—	—	
Sonchus arvensis	—	—	—	—	
Leontodon autumnalis	—	—	—	—	

ed)

arshes of Skallingen

			Saginetum maritimae								
	56084	56086	56074	56068	56082	56080	56073	56087	56085	56081	56088
	2×8	2×6	3×5	3×6	4×6	8×12	3×6	3×4	3×5	3×6	4×8
	100	100	95	90	80	70	45	35	20	15	10
	—	—	—	+.1°	—	+.1°	+.1°	—	—	+.1°	—
	—		—		—	—	—	—	—	—	
	—		—	—	—	—	—	—	—	—	—
	+.2	—	1.2	+.1	+.1–2		—	—	—	—	
	—	—	1.1–2	1.1–2	2.2	1.1–2	2.2	+–1.1	+.1–2	+–1.1–2	—
	—	—	—	+.1	1–2.1	+.1	—	+–1.1	+.1	2.1–2	+.1
	—	—	+.1°	+.1°	+.1°	+.1°	+.1°	—	—	+.1°	—
	—	—	—	+.1°	—	+.1°	1.1°	—	—	—	—
	—	—	—	—	—	+.1°	+.1°	—	—	—	—
	—	—	—	—	—	—	—	—	—	—	—
	—	+.1	+.1–2	+–1.1	2.1	2.1–2	1–2.1–2	2.1–2	2.1–2	1.1–2	1–2. 1–2
	—	—	—	—	—	—	+.1	+.1	+.1	—	—
	—	—	—	—	—		—	—	—	—	—
	+.1	1.1–2	—	—	+.1	—	—	—	—	—	—
	—	+.1	—	—	+.1	—	—	—	—	—	+.1
	+.1	+.1	—	—	—	—	—	—	—	—	—
	+.1	+.1	+.1°	+.1°	+.1°	+.1°	+.1°	—	—	—	—
-2	+.1	+.1	1.1	2.1–2	+.1	2.1	1–2.1–2	1.1	1.1–2	1.1	+–1.1
	5.5	5.5	5.5	5.5	4.5	4.5	3.5	2–3.5	2.2	2.2	2.1–2
	+.1	+.2	+.1–2	+.2	+.2	1–2.2	1.1–2	+.1	+.2	+–1.1–2	+.2
	+.1	+.1	—	—	—	—	—	—	—	—	—
	—	—	—	+–1.2	+.2	1–2.2	1.2	—	—	—	—
	—	—	—	—	+.1	—	—	—	—	+.1	+.1
	—	—	—	—	+.2	—	—	—	—	—	—
	—	—	—	—	1.2	—	—	2.2	1.2	1–2.2	—
	—	—	—	—	—	+.1	—	—	—	—	1.1
	—	—	—	—	—	—	—	2.1–2	—	—	—
	—	—	—	—	—	—	—	+–1.1	—	—	—
	—	—	—	—	—	—	—	+.1	—	—	—
	—	—	—	—	—	—	—	+–1.1	+.1	—	—
	—	—	—	—	—	—	—	—	+–1.2	—	+.2
	—	—	—	—	—	—	—	—	—	+.1	—
	—	—	—	—	—	—	—	—	—	—	+.1
	—	—	—	—	—	—	—	—	—	—	+.1

maritimum, *Suaeda maritima* and *Spergularia marginata* are very sparse or entirely lacking.

On the banks a *Festuca rubra* sward is found with scattered individuals of *Artemisia maritima*, *Halimione portulacoides*, *Limonium vulgare* and *Plantago maritima*. Of the latter both the *var. dentata* and the typical form occur. This vegetation belongs to the *Artemisietum maritimae* (HOCQUETTE 1927) BRAUN-BLANQUET et DE LEEUW 1936 em. WEEVERS 1940.

The synsystematics of the *Artemisietum maritimae* offer interesting problems. CHRISTIANSEN (1927) has described the association without giving it a name; VAN LANGENDONCK (1931, 1933) distinguished the "association à *Artemisia maritima* et *Statice Limonium*"; BRAUN-BLANQUET and DE LEEUW (1936) and afterwards TÜXEN (1937) the "*Artemisia maritima-Obione portulacoides* Assoziation (*Artemisietum maritimae*)" with *Artemisia maritima*, *Obione portulacoides*, *Parapholis strigosa* and *Limonium vulgare* as supposed faithful species; VLIEGER and ADRIANI (1938), ADRIANI (1945) and WESTHOFF (1947) reduced the faithful species to three, viz. *Artemisia*, *Halimione* and *Limonium*. The first who broke with this view was WEEVERS (1940), considering *Halimione* and *Limonium* faithful species of the *Puccinellietum maritimae*. Afterwards, TÜXEN (1957) goes in this direction, however considering *Halimione* a species characteristic for the order *Juncetalia maritimi*. The author sides with WEEVERS taking only *Artemisia* as faithful species of the association.

Essentially the cause of this misunderstanding may be the poor development of the *Artemisietum maritimae* in the Wadden Sea area. This poor development is due (1) to the chiefly very sandy character of the soil and (2) on those localities where more fine material was deposited, to the absence of tidal creeks with banks, usually offering well-aerated soil conditions and a slightly clayish character of the soil. If the association occurs it has often a floristic composition related to the *Armerion maritimae* (CHRISTIANSEN, 1927; BRAUN-BLANQUET and DE LEEUW, 1936; TÜXEN, 1937; WESTHOFF, 1947; TÜXEN, 1957). However, Skallingen shows that in the Wadden Sea area the association can develop completely under favourable sedimentation conditions and along well-evolved tidal creeks. On that marsh it resembles the corresponding phytocenoses in the S.W.-Netherlands to a high degree: it lacks elements of the *Armerion maritimae* and therefore it belongs to the alliance *Puccinellion maritimae*.

Table I shows the ecological amplitudes of the three above mentioned species in the series of the outer salt marshes. *Limonium vulgare* has its optimum in the transition of *Puccinellietum maritimae* to *Halimionetum portulacidis* and in the lower parts of the latter. The character of its amplitude — the height and range of a constructed bell-shaped curve along the environmental gradients — accounts for its position of faithful species of the alliance *Puccinellion maritimae*. (Compare also table II). Under well-aerated soil conditions mainly involved in the development of banks along tidal creeks *Halimione portulacoides* forms a zone above the *Puccinellietum maritimae* and below the *Festuca rubra*-

sward. According to its high optimum in comparison with the range of its amplitude it seems better to segregate the *Halimionetum portulacoidis* like English and French authors do (CHAPMAN, 1934; TANSLEY, 1939, 1949; DES ABBAYES and CORILLON, 1949; CORILLON, 1953). According to these references and the present data of Skallingen the *Halimionetum* has a wide distribution occurring from Denmark southwards perhaps to the coast of Spain and, fragmentary (?), to Portugal (FONTES, 1945). Finally, the optimum of *Artemisia maritima* is found in the *Festuca rubra*-sward on the banks along the tidal creeks and, locally, in the upper part of the *Halimionetum portulacoidis*. The range of its amplitude is very small. Therefore it seems better to consider only that species as faithful to the *Artemisietum maritimae* following the above discussed view of WEEVERS (1940). Local occurrence of *Artemisia maritima* in the upper part of the *Halimionetum* may then lead to distinction of a terminal phase with *Artemisia* in this association. Likewise in the *Artemisietum maritimae* an initial phase with co-dominance of *Halimione* may be distinguished.

Besides the *Artemisietum maritimae* a vegetation with *Agropyron litorale* (Host.) Dum. 1823 (= *Agropyron pycnanthum* (Godr.) Gren. et Godr. 1855/56 = *Elytrigia litoralis* (Dum.) Hyl. 1945) as dominant species may be found on the banks (leg. W. G. Beeftink, Herb. Hydrobiol. Inst. afd. Delta-onderzoek nr 244). According to HANSEN (1945, 1958), discussing its systematics and distribution along the German North Sea coast, the most northern record was from the isle of Fanø. During the present investigation of Skallingen one well-developed phytocenose has been found in which this species is dominant (analyse 56041, Table I). On another bank a few individuals of the species have been discovered occurring in the *Artemisietum maritimae*. This phytocenose, which here may be considered provisionally as a sociation with *Agropyron litorale* of the alliance *Puccinellion maritimae* occurring southwards to the west coast of France, is also an important indicator of the abiotic environmental processes at work on the peninsula. In section 4 the interpretation of this phenomenon will be discussed.

Concerning the classification of the associations into higher floristically defined vegetation units the author agrees with the view of TÜXEN (1937, 1952) who separates the *Salicornia*-associations from the proper salt marsh vegetations. Therefore the distinction of the alliances *Thero-Salicornion* BRAUN-BLANQUET 1930 and *Puccinellion maritimae* (CHRISTIANSEN 1927 p.p.) TÜXEN 1937 is preferred to the *Puccinellio-Salicornion* BRAUN-BLANQUET et DE LEEUW 1936. However, the assertion of BRAUN-BLANQUET and TÜXEN (1952, p. 273) that these alliances can be separated completely according to ecological factors except the salt factor, cannot be accepted. Typical differences in floristic composition should be considered here and other criteria than the fidelity of species ought to be involved.

3.2. *The inner salt marshes*

The lower places of the inner marshes do either not bear any vegetation of Phanerogams or they are covered with scattered individuals of *Salicornia europaea*, perhaps presenting another form than those of the outer marshes (compare König, 1939 and Christiansen, 1955). The adjacent *Puccinellietum maritimae*, here too, may be divided into two phases (Table II): the lower one linking with the *Salicornietum europeae* and rich in the therophytes *Suaeda maritima* and *Salicornia europaea*, the higher phase with optimal development of *Limonium vulgare* and *Plantago maritima* (the typical form and the *var. dentata* Bl. et Fing.). Therefore the character of the phytocenoses differs from that of the *Puccinellietum maritimae* of the outer marshes. Moreover, *Spergularia marginata* has a greater presence and *Aster tripolium* a greater cover in the first mentioned habitat. On the other hand *Halimione portulacoides* occurs with a smaller cover and, generally, it has a rather more reduced vitality. Finally, physiognomically the association of the inner marshes stands out owing to the reddish colour of *Puccinellia maritima*. All those differences and also the occurrence of *Festuca rubra* and *Glaux maritima* in the high parts of the inner salt marsh association are connected with diversities in soil conditions, particularly the granular composition related to water and salt properties.

The *Puccinellietum maritimae* extends up to the foot of the sandhills. The frequently steep slopes of these hills are covered with a dense turf of *Festuca rubra* sometimes preceeded by a zone — up to about 25 cm — where *Juncus gerardi* is dominant or co-dominant. This narrow *Juncus*-strip of which no analyses has been made, is only found where stagnating water can occur in the *Salicornia* and *Puccinellia* vegetation. The rainspell combined with a storm flood of the preceding days showed this relation very clearly.

In the *Festuca* vegetation *Armeria maritima* is found very sparsely and in the upper zone only. In the whole country of Denmark the species has been observed on higher localities, mostly in and above the storm flood zone. Moreover, in the interior of Jutland it grows rather frequently in habitats, such as sandy areas with heath vegetation (Iversen, 1936). This phenomenon is one of the arguments why the name of *Armerieto-Festucetum* Braun-Blanquet et De Leeuw 1936 does not suit this most important association of the spring-tide zone. Westhoff also pointed to the necessity of re-interpretation of the alliance *Armerion maritimae* (Westhoff and Van Leeuwen, 1958). Therefore it seems preferable to use the older name of *Juncetum gerardi* (Warming 1906), Tüxen 1957. On Skallingen the association shows an affinity to the *Junceto-Caricetum extensae* Braun-Blanquet et De Leeuw 1936 because of the presence of *Carex extensa*.

In the above mentioned *Festuca* vegetation, in the following *Saginetum maritimae* and in the *Artemisietum maritimae* of the outer marshes *Festuca rubra* (leg. W. G. Beeftink, Herb. Hydrobiol. Inst. afd. Delta-onderzoek nr 226) conforms to the description of *f. litoralis* given by Hackel (1882, p. 139) and Weber (1892, p. 212). Although concise the description of Hackel[1]) is clear, consequently the author's name of

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[1]) Hackel (1882, p. 139): forma litoralis humilis, valde repens, panicula brevi (2–4 cm lg.) compacta.

C. A. Weber given by WESTHOFF (1947, manuscript) and TÜXEN (1957), ought to be replaced by Hackel. According to Ir R. DUYVENDAK (verbal communication) who studied the systematics of *Festuca* species, *Festuca rubra f. litoralis* Hack. 1882 clearly differs from *var. genuina* Hack. *subvar. vulgaris* (Gaud.) Hack. and *subvar. arenaria* (Osb.) Hack. Therefore it is justified to maintain the distinction which has been drawn by Hackel and Weber.

Finally the open vegetation at the top of the sandhills belongs to the *Saginetum maritimae* WESTHOFF 1947. From the three faithful species, *Sagina maritima*, *Plantago maritima var. leptophylla* M. et K. and *Pottia heimii*, only the first two were observed. However, according to ROMOSE (1938), *Pottia heimii* does occur in this association on Skallingen. Probably its occurrence in the analysed vegetations was prevented by high winds blowing away the sand. In the *Saginetum maritimae* a very outstanding form of *Agrostis stolonifera* was observed (leg. W. G. Beeftink, Herb. Hydrobiol. Inst. afd. Delta-onderzoek nr 245). Its stiff shoots and leaves are erect. The plants form little tufts of characteristic withered appearence. The most striking feature however, is the missing of rhizomes and stolons. It is not sure whether the form has a genetic status. Perhaps the, above mentioned, high winds, blowing away the dry sand, may have been instrumental in creating this modification. Probably this form is not found in the Netherlands up to now. IVERSEN (1936) has described it under the name *A. stolonifera var. stricta*. It is doubtful whether this name can be maintained for it was often used previously in the systematic literature on *Agrostis stolonifera*.

4. DYNAMICS OF THE VEGETATION IN CONNECTION WITH ENVIRONMENTAL DEVELOPMENT

The thorough investigation of Skallingens salt marsh vegetation by IVERSEN (1936) in 1931–'34, his comparison of the vegetation at this time with that of 20 years later (IVERSEN, 1952/53), together with the author's investigations, offer a good base for some conclusions about its dynamics in relation to environmental changes in this century and for a prognosis about its future development. However, it is necessary to make restrictions: The investigations of Iversen refer to the vegetation of the whole peninsula and those of the present author only to a part of it. Moreover, the investigation methods of Iversen and the present author are different. Therefore it seems indicated to simplify the data so that a rough classification into three groups of combined cover degree-abundance (BECKING, 1957) — Fr.: dominance-abundance, Ge.: Dominanz-Abundanz — may be made. The author's classification is as follows:

(1) combined cover degree-abundance + and 1, the latter only when presence is evidently smaller than 100 % (dotted lines in Table III);
(2) combined cover degree-abundance 1 and 2 (drawn lines) and
(3) combined cover degree-abundance 3, 4 and 5 (cross-striped lines).

Likewise the data of IVERSEN (1936, 1952/53) from the years 1931–'34 are fitted in these groups by estimation as best as possible.

The halophytic vegetrtion of Ska

The outer salt marshes

Associations in 1931–'34	Salicornietum europaeae	Puccinellietum maritimae variant with Halimione pedu initial phase	phase with Suaeda and Aster	phase with nium and H
Associations in 1956	**Salicornietum europaeae**	**Puccinellietum maritimae initial phase**	**optimal phase**	**Halimion portulac**
Salicornia europaea.	— r + r r r + r +	+ r r r r r r : r	r r r — — — —	— — — —
	——— + + +	+ + + + + + + + +	+ + + + + + + ——	— — — -
Puccinellia maritima	—	— + r r r + r + +	r r r r r r r r r	+ r + r +
	—	—— + + + + + +	+ + + + + + + + +	—— — —
Halimione pedunculata		— — — — —	————	— — — -
Halimione portulacoides.		— — — — — —	———— +	+ + + + + -
Artemisia maritima				—
				—
Agropyron litorale				
Spartina townsendii.	— —— — — -	- ——— —— -	— —	
Aster tripolium		— — ———	+ + + + + + + + +	————
		— — ———	————	—
Suaeda maritima		— ——— + + +	+ + + + + + + + +	+ + — — -
	—	—— + + — + + + —	— + + — + + — + +	— — — -
Spergularia marginata		— —	— — —— ——	————
		— —	— — —	
Triglochin maritimum			— — — —	— — — -
		— ————	— — — — — —	— — -
Limonium vulgare			— — — ——	————
		— — — — ——	— — — — —— +	+ + + + + -
Plantago maritima			— — — — — -	— + + + + +
			— —	————
Festuca rubra				—
				—
Glaux maritima			— — — —	— — — -
Juncus gerardi				
Armeria maritima				

(the upper lines) 1956 *(the lover lines).*

	The inner salt marshes				
		Puccinellietum maritimae			
nisietum itimae	Salicornietum europaeae	phase rich in therophytes	phase with Aster and Plantago	Juncetum gerardi	Saginetum maritimae
		Puccinellietum maritimae			
nisietum ritimae	Salicornietum europaeae	phase rich in therophytes	phase with Limonium and Plantago	Juncetum gerardi	Saginetum maritimae
	——+++++++	+++++++++	+++—— — —	— —	—
	——+++++++	+++++++++	+++—— — — -		— — — — —
	— — —	+++++++++	+++++++——	—	
	— — —	++-++-+++	+++++++——		
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		— — — — ——	++++++++—	———— — —	
		— — — — ——	————	— —	
	— —	————— —	— — — — —	— —	—
	— —	————— —	— — — — — —		— —
-		— - . ——	————	—	
		— — — ——	—— — — ——		
		— — — ——	————	———— — —	—
		- — — — — —	— — —— — —	— — — —	
— —		— — — - —	— — —— —	— — — — —	
————		— — — — ——	——++——+++	———— — —	— — — —
+++++		— —	— — — ——++	—— — - — —	————
— — — —		— —	— — ——++	—— — — — —	————
+++++			— — —	+++++++++	+++++++——
+++++			— — —	+++++++++	+++++++——
— — — —			— — — — —	— — — — — —	— — — —
			— — —		
— — — —			—	++— — — — —	— — — —
				++—— — — —	— — — —
— - —				— —	— — ——
				— —	— — ——

The changes in the abiotic environment discussed in the second section induce the vegetation to react: (1) with extension or shrinking of the potential ecological amplitudes of taxa directly consequent on changes of abiotic habitat factors in favourable resp. unfavourable sense; (2) with disturbing the equilibrium in the mutual influences of individual organisms and taxa due to changes in competition power in consequence of (1) and resulting in shifting the actual ecological amplitudes. Without experiments these two aspects cannot be distinguished in vegetational changes and therefore we are now only able to make some suppositions.

In Table III the most important halophytes have been assembled with their actual ecological amplitudes and optima in 1931–'34 (the upper lines) and in 1956 (the lower lines). The most striking feature is the invasion of *Halimione portulacoides*. According to GABRIELSEN and IVERSEN (1933) in 1909, when Raunkiaer studied the vegetation of Skallingen, this species was not observed. In 1931 a few specimens were discovered and in the following years the number greatly increased (GABRIELSEN and IVERSEN, 1933). Nowadays *Halimione* is very abundant, especially in a zone between *Puccinellia maritima* and *Festuca rubra*. According to HULTÉN (1950) it reaches its northern limit on Skallingen and consequently it might be supposed that its area had extended in the last decennia as a consequence of climatic factors. Yet the author is inclined to attribute its extension on the outer marshes mainly to favourable conditions of sedimentation. The study of salt marsh vegetation in the S.W.-Netherlands indicated that *H. portulacoides* prefers well-aerated silty banks along tidal creeks. In the Wadden Sea from the Netherlands till Denmark these banks are generally rare and so the species is but sparsely presented there. Once established it is able to endure accumulation of sand very well (CHAPMAN, 1934 and the author's experience). Its extension in the inner marshes might be connected with sedimentation also, but probably the actual presence of an important centre of diaspores in the outer marshes preponderates here while sedimentation of silt is insignificant.

Halimione pedunculata — another "halophyte pur sang" — has its optimal development in the salt steppes of Central Europe, especially those of Germany (WESTHOFF, 1947 manuscript; WENDELBERGER, 1950). The western and northern limit of its geographical area is reached on the Atlantic and Baltic coasts. On Skallingen it had its optimum in the *Puccinellietum maritimae*, while it also regularly occurred in the *Artemisietum maritimae*, *Juncetum gerardi*, *Junceto-Caricetum extensae* and *Saginetum maritimae* but with very little frequency (IVERSEN, 1936 p. 187–193). Its coastal occurrence depends on the presence of an open vegetation which is often connected with a sandy substratum. It is not sure which factor preponderates but according to WESTHOFF (1947, manuscript) it may be the first one. Sedimentation of silt promotes a dense growth of *Puccinellia maritima*, especially when there is no intensive grazing. This phenomenon combined with the increased competition power of *H. portulacoides* may have caused the disappearance of *H. pedunculata* in the investigated strip.

Next to *H. portulacoides Limonium vulgare* has spread very much. Its favourable reaction on sedimentation of silt seems evident on the outer marshes but does not give a sufficient explanation of the extension on the inner marshes. The creation of a centre of diaspores on the first ones may be a factor but its effect is perhaps not as marked as in the case of *H. portulacoides* owing to the fact that the initial population of 1931–'34 was only slightly smaller than the present one. The competition power of *Limonium vulgare* is large, for it was able to extend having an optimum which strongly coincides with that of *H. portulacoides*. However, the analyses 56053 and 56055 ought to be considered as transitions in time and not geographically, starting from a terminal phase with *Limonium* and *Plantago* of the *Puccinelietum maritimae* to the *Halimionetum portulacoidis*. The third species which prefers silty soils is *Artemisia maritima* but only to a certain extend as will be pointed out further on.

The extension of *Halimione portulacoides* and *Limonium vulgare* may result in a shrinking of the ecological amplitude of *Puccinellia maritima*, *Aster tripolium*, *Suaeda maritima*, *Spergularia marginata* and *Plantago maritima* on the outer marshes and of *Aster tripolium*, *Spergularia marginata* and *Triglochin maritimum* on the inner marshes. Except for *Plantago maritima* probably the changed soil texture conditions are not important, for these species seem to be fairly indifferent in this respect (for *Aster* compare CLAPHAM, PEARSALL and RICHARDS, 1942). The large frequency of *Triglochin maritimum* in 1931–'34 on the inner marshes compared with that on the outer marshes points to local stagnant water in the first mentioned marshes, a phenomenon already indicated in section 3.2 in connection with *Juncus gerardi*. Therefore it is possible that the ecological amplitude of *Triglochin* on the inner marshes was more influenced by those soil water conditions than by the increased competition power of *Halimione* and *Limonium*. Likewise the extension of *Triglochin* on the outer marshes may be explained by the larger water content of the soil, a result of the more clayey character. Compared with the situation in 1931–'34 *Salicornia europaea* has extended on somewhat higher levels. This phenomenon, too, may be connected with progressive sedimentation during the last decennia, the result of this proces being a changed granular composition of the upper soil layers promoting a slightly higher salt content of the soil-liquid, owing to reduced leeching of salts in the, now heavier, soils.

In 1931–'34 the *Artemisietum maritimae* showed a floristic composition related to the *Armerion maritimae* on account of the occurrence of *Glaux maritima*, *Juncus gerardi* and *Armeria maritima*, which last three species are absent today in the investigated part of the outer marshes. At present, on isolated localities, *Agropyron litorale* is superseding the *Artemisietum maritimae*. In the S.W.-Netherlands the author encountered *Agropyron litorale* ousting the *Artemisietum maritimae* on localities, where the banks were silted up with much fine material. These floristic changes may therefore be regarded as results of the heavier character of the soils along the banks of the tidal creeks, as described earlier.

On the outer marshes the following synecological trends may be considered as a reaction on environmental development: (1) A transition of the final phase of the *Puccinellietum maritimae* with *Limonium* and *Plantago* as co-dominants into the *Halimionetum portulacoidis*. (2) A more optimal development of the *Artemisietum maritimae* on account of the disappearance of elements of the *Armerion maritimae*. (3) At a few localities the establishing of a sociation with *Agropyron litorale* from the *Artemisietum maritimae*.

On the outer marshes sedimentation of silt has already made great progress. Owing to the relatively high position of the marshes related to MHW-level only high floods mostly combined with storms are able to cover the marshes. The feature of these floods is a mostly very turbulent condition of the water. Therefore the proportion between sand and silt of the material deposited will shift in favour of the sand fraction the higher the marshes have been built up, for silt is only able to settle in relatively calm water. For this reason it is to be expected that on the outer marshes of Skallingen in the future the material deposited will increase its sandier character once more in some degree. The expansion of *Agropyron litorale*, depending to a great extend on a relatively high silt content of the banks, will therefore probably remain confined to a few banks unless the existence of centres of diaspores enables the species to conquer the banks in spite of the *Artemisietum maritimae*. The latter progress, however, depends on the granular composition of the bank soils which was not studied. Finally, we may expect the *Halimionetum portulacoidis* to develop still further especially at the cost of the *Puccinellietum maritimae*, at present in the basins growing in its optimal phase.

On the inner marshes the modification of the floristic composition of the associations is less spectacular than on the outer marshes. Possibly only the increase of *Limonium vulgare* and the decrease of *Aster tripolium* will necessitate a change in the denomination of the highest situated phase of the *Puccinellietum maritimae*. Owing to the limited extend of these changes it is not to be expected that the vegetation of the inner marshes will change much in the future.

SUMMARY

During the excursion of the International Society for Plant Geography and Ecology in 1956 the author was in a position to stay some days at Skalling-Laboratory to study the salt marsh vegetation of the Peninsula (Fig. 1). In the past 25 years silt has been deposited mainly on a strip along the Wadden Sea coast, the so-called outer marshes. These sedimentation conditions have created a bank-and-basin-landscape (Fig. 2). The inner marshes have been modificated only slightly in this respect.

The vegetation of an ungrazed strip overlapping both outer and inner salt marshes is described in detail. On the outer marshes the following communities are distinguished: *Zosteretum nanae* (fragmentary), *Salicornietum europaeae*, *Puccinellietum maritimae* divided into an initial and an optimal phase, *Halimionetum portulacoidis*, *Artemisietum maritimae* and very scarcely, a sociation with *Agropyron litorale*, a species which is new for Skallingen. The different views about synsystematic limitation of the *Artemisietum maritimae* are discussed in detail; the author agrees with the view of Weevers (1940). From the inner marshes are described: *Salicornietum europaeae*, *Puccinellietum maritimae* divided into a phase rich in therophytes and a phase with *Limonium vulgare* and *Plantago maritima*, *Juncetum gerardi* and *Saginetum maritimae*. The taxonomy of the forms of *Festuca rubra* and *Agrostis stolonifera* occurring on these

marshes is discussed briefly. Arguments for a change of the association's name from *Armerieto-Festucetum* to the older name of *Juncetum gerardi* are tentatively proposed. A separation of the *Puccinellio-Salicornion* into the alliances *Thero-Salicornion* and *Puccinellion maritimae* is preferred and discussed briefly.

The vegetation was found to react to changes in the environment with the establishment and extension of *Halimione portulacoides* and the extension of *Limonium vulgare* and *Artemisia maritima*. *Halimione pedunculata* disappeared as well as *Glaux maritima*, *Juncus gerardi* and *Armeria maritima* in the *Artemisietum maritimae*. On the outer marshes species decreasing their ecologic amplitude and partly their cover are *Puccinellia maritima*, *Aster tripolium*, *Suaeda maritima*, *Spergularia marginata* and *Plantago maritima*. Contrary to the above mentioned species *Salicornia europaea* and *Triglochin maritimum* have extended on the outer marshes in consequence of progressive sedimentation resp. changed soil water conditions.

Finally synecological trends have been discussed. The most important ones are the development of the *Halimionetum portulacoidis* and the establishment of a sociation with *Agropyron litorale* on the outer salt marshes. It is expected that these trends will proceed on a limited scale in the future.

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REFERENCES

Adriani, M. J. 1945. Sur la phytosociologie, la synécologie et le bilan d'eau de halophytes. S.I.G.M.A. Comm. **88**: 1–217.

Becking, R. W. 1957. The Zürich-Montpellier school of phytosociology. Bot. Review **23**: 411–488.

Braun-Blanquet, J. 1951. Pflanzensoziologie. Grundzüge der Vegetationskunde. Wien, Springer, 631 pp.

——— and W. C. de Leeuw. 1936. Vegetationsskizze von Ameland. Ned. Kruidk. Arch. **46**: 359-393.

——— and R. Tüxen. 1952. Irische Pflanzengesellschaften. Veröff. Geobot. Inst. Rübel, Zürich. **25**: 224-421.

Chapman, V. J. 1934. In J. A. Steers (ed.): Scolt Head Island, 77-145.

Christiansen, W. 1927. Die Auszendeichsvegetation von Schleswig-Holstein mit besonderer Berücksichtigung von Föhr. Föhrer Heimatbüchern **16**: 1–29.

——— 1955. Salicornietum. Mitteil. Flor.-soziol. Arbeitsgem. **5**: 64–65.

Clapham, A. R., W. H. Pearsall and P. W. Richards. 1942. Aster tripolium. Jour. Ecol. **30**: 385-395.

Corillion, R. 1953. Les Halipèdes du Nord de la Bretagne. Rev. Gén. Bot. **60**: 609–658 and 707–775.

Des Abbayes, H. and R. Corillon. 1949. L'Obionetum des halipèdes du Nord de la Bretagne (Finistère à Ille-et-Vilaine). C. R. Séances Acad. Sci. **228**: 935–937.

De Smet, L. A. H. 1954. Enkele opmerkingen over kalkarme zeeklei-afzettingen. Boor en Spade **7**: 169-173.

De Vries, D. M. 1935. Plantengezelschappen als kenteeken van het keukenzoutgehalte van de bodem. Ned. Kruidk. Arch. **45**: 97–121.

Fontes, F. C. 1945. Algumas caracteristícas fitosociológicas dos "salgados" de Sacavém. Bol. Soc. Brot. **19**: 791–813.

Gabrielsen, E. K. and J. Iversen. 1933. Die Vegetation der Halbinsel Skallingen. I. Die Flora von Skallingen. Dansk Bot. Tidsskr. **42**: 355–383.

HACKEL, E. 1882. Monographia Festucarum europaearum. Kassel and Berlin, Th. Fischer, 216 pp.

HANSEN, A. 1955. Elytrigia (Agropyron) litoralis (Dum.) Hyl. und ihr Vorkommen an der deutschen Nordseeküste. Mitteil. Arbeitsgem. Schleswig-Holstein und Hamburg **5**: 60–66.

————. 1958. Noter om danske planter II. Bot. Tidsskr. **54**: 170–175.

HULTÉN, E. 1950: Atlas of the distribution of vascular plants in the N.W.-Europe, Stockholm, Generalstadens Litografiska Anstalts Forlag, 512 pp.

IVERSEN, J. 1936: Biologische Pflanzentypen als Hilfsmittel in der Vegetationsforschung. Medd. Skalling-Lab. **4**: 1–224.

————. 1952/53. The zonation of the salt marsh vegetation of Skallingen in 1931–34 and in 1952. Geogr. Tidsskr. **52**: 113–118.

JAKOBSEN, B. 1952/53. Landskabsudviklingen i Skallingmarsken. Geogr. Tidsskr. **52**: 147–158.

JØRGENSEN, C. A. 1934. Plantningsforsøg med Spartina Townsendii i den danske Vester havsmarsk. Bot. Tidsskr. **42**: 420–440.

KÖNIG, D. 1939. Die Chromosomenverhältnisse der deutschen Salicornien. Planta **29**: 361–375.

NIELSEN, N. 1935. Eine Methode zur exakten Sedimentationsmessung; Studiën über die Marschbildung auf der Halbinsel Skalling. Medd. Skalling-Lab. **1**: 1–98.

RIVIÈRE, A. 1942. Données experimentales sur les conditions physico-chimiques de la sédimentation ferrugineuse en milieu marin. C. R. Somm. Séances Soc. Géol. France: 200–201.

ROMOSE, V. 1938. Undersøgelser over Skallingens Mosflora. Bot. Tidsskr. **44**: 439–458.

SANDERS, P. and B. VERHOEVEN. 1956. Verslag over een reis ter bestudering van de landaanwinning in West-Duitsland en Jutland. Report Werkgroep Commissie Landaanwinning T.N.O., 69 pp.

TANSLEY, A. G. 1939 and 1949. The British Islands and their vegetation, 2 tomes. Cambridge, Univ. Press, first ed. 968 pp, second ed. 930 pp.

TÜXEN, R. 1937. Die Pflanzengesellschaften Nordwestdeutschlands. Mitteil. Flor.-soziol. Arbeitsgem. Niedersachsen **3**: 3–170.

————. 1957. Die Pflanzengesellschaften des Auszendeichslandes von Neuwerk. Mitteil. Flor.-soziol. Arbeitsgem. **6/7**: 205–234.

VAN DER SPEK, J. 1952. Over het verdwijnen van koolzure kalk uit zeekleiafzettingen tengevolge van de oxydatie van hierin aanwezige sulfiden. Landbouwk. Tijdschr. **64**: 473–478.

VAN LANGENDONCK, H. J. 1931. Inleiding tot de phytosociologische studie der schorren. Natuurwet. Tijdschr. **13**: 203–229.

————. 1933. La sociologie végétale des schorres du Zwyn et de Philippine. Bull. Soc. Roy. Bot. Belgique **65**: 112–136.

VERHOEVEN, B. 1954. Enkele opmerkingen over de groei van de schorren in de Brakman. In: A. J. ZUUR, ed.: Langs gewonnen velden. Facetten van Smedings werk, Wageningen, Veenman en Zn., 88–95.

VLIEGER, J. and M. J. ADRIANI. 1938. Plantensociologische aanteekeningen in oostelijk Zeeuwsch-Vlaanderen. Ned. Kruidk. Arch. **48**: 35–43.

WEBER, C. 1892. Über die Zusammensetzung des natürlichen Graslandes in Westholstein, Dithmarschen und Eiderstedt. Schr. natürwiss. Ver. Schleswig-Holstein **9**: 179–217.

WEEVERS, TH. 1940. De flora van Goeree en Overflakkee dynamisch beschouwd. Ned. Kruidk. Arch. **50**: 285–354.

WENDELBERGER, G. 1950. Zur Soziologie der kontinentalen Halophytenvegetation Mitteleuropas. Denkschr. Österr. Akad. Wissensch. **108** (5): 1–180.

WESTHOFF, V. 1947, manuscript. The vegetation of dunes and salt marshes on the dutch islands of Terschelling, Vlieland and Texel.

————. 1947. The vegetation of dunes and salt marshes on the dutch islands of Terschelling, Vlieland and Texel, 's Gravenhage, Van der Horst, 131 pp.

———— and CHR. G. VAN LEEUWEN. 1958. Verslag van een studiereis naar Duitsland. Report State Inst. for Nature Conservation Research (R.I.V.O.N.), Bilthoven, the Netherlands, 12 pp.

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NOMENCLATURAL NOTES ON THE GENERA DALZELLIA, LAWIA, MNIANTHUS, AND TERNIOLA (PODOSTEMACEAE)

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(*received March* 19*th*, 1959)

In 1846 GARDNER described *Tristicha zeylanica* based on material collected in Ceylon. TULASNE, however, in 1849, in his precursor to a monograph of the *Podostemaceae*, transferred this species to his new genus *Lawia*, adding, moreover, *L. pulchella* and *L. longipes*.

In 1852, TULASNE, apparently having discovered that his *Lawia* was antedated by *Lawia* Wight of 1847, transferred the three species to *Terniola*. Wight's *Lawia* later turned out to be a later synonym of the rubiaceous *Adenosachme*.

In the same year, January 1852, WIGHT placed the species of *Lawia* known to him — in this case *L. zeylanica* (Gardner) Tul. only — in his new genus *Dalzellia*, adding *D. foliosa* Wight, *D. lawii* Wight, *D. pedunculosa* Wight and *D. ramosissima* Wight.

Also in the year 1852 WALPERS placed Tulasne's three species of *Lawia* in *Mnianthus* as *M. zeylanicus* (Gardner) Walpers, *M. pulchellus* (Tul.) Walpers and *M. longipes* (Tul.) Walpers. It is evident from Walpers text that he did not yet know Tulasne's paper of 1852 or that this paper was not yet published at the time of publication of Walpers' book. As far as can be traced Walpers Annales must have been published before April the 8th, 1852, since in the Oesterreichische Botanische Wochenblatt, 2nd year, Nr 14, on page 118, is referred to Walpers' book as being recently published.

In an attempt to establish the priority of any of the three homotypic synonyms over the other I tried to find the date of publication of Tulasne's paper of 1852. The National Library of France nor the Museum of Natural History in Paris were able to give me the exact date of publication however. Therefore, since one of the three dates of publications of 1852 is unknown one is left free to make a choice in regarding one of the names as a valid one, provided earlier authors did not make this choice before.

For that we have to turn to WEDDELL's paper of 1873 and WARMING's paper of 1901.

WEDDELL in 1873 unites *Terniola* Tulasne, *Dalzellia* Wight and *Mnianthus* Walpers to one genus for which he chooses the name *Terniola*. Seven species are included, viz *T. foliosa* (Wight) Wedd., *T. lawii* (Wight) Wedd., *T. longipes* (Tul.) Tul., *T. pedunculosa* (Wight) Wedd., *T. pulchella* (Tul.) Tul., *T. ramosissima* (Wight) Wedd., and *T. zeylanica* (Gardner) Tul.

With this choice it is well established that the generic name *Terniola* Tulasne should be used to include the species of the genera *Dalzellia*, *Lawia*, *Mnianthus* and *Terniola*.

As regards to the type species of *Terniola* we can find in WARMING's paper of 1901 a reference to this. Here he indicates *Lawia zeylanica* as the type species of *Lawia*, but on the other hand he indicates *Terniola foliosa* as the type species of *Terniola*. To this can be remarked that the last typification is not a correct one since under the present-day rules of nomenclature a type species can only be indicated from among the species originally described in that genus. In this case *Terniola foliosa* is inserted in *Terniola* by Weddell in 1873 based on *Dalzellia foliosa* Wight and the original *Terniola* of Tulasne did not include *T. foliosa* at all.

Actually nomenclatorally it is not important which species Warming indicated as being the type species of *Lawia* and *Terniola*, since a later study of WILLIS showed that both species (*Lawia zeylanica* and *Terniola foliosa*) are conspecific and as *Lawia zeylanica* is based on *Tristicha zeylanica* of 1846 and *Terniola foliosa* is based on *Dalzellia foliosa* of 1852 the specific epithet *zeylanica* is the one to be used. Therefore we have to regard *Terniola zeylanica* (Gardner) Tulasne as the type species of the genus *Terniola*.

Weddell's conception of *Terniola* is, however, too large and we have to exclude *T. ramosissima* (Wight) Weddell. This species consists of long, creeping roots from which arise long, slender, often branched shoots with linear, scattered leaves, while all the other species of *Terniola* (now representing only one, highly variable species) have lichen-like expanded roots from which very short shoots arise with the leaves densely conferted at the tip of the shoots. As no generic name is available to be applied to a genus including this species the new name *Indotristicha* is used, referring to the form of the plant which resembles a true *Tristicha* species, but differing from that genus by the three stamens and the cupular-like organ which is formed by connate leaves at the base of the pedicel. Moreover the genus *Tristicha* is restricted to America and Africa and as this new genus is found in India this explains the use of the first part of the new generic name.

Concluding this paper the synonymy and literature of the two remaining genera are given.

1. **Indotristicha** van Royen, novum genus* — *Dalzellia* Wight, Icon. Pl. Ind. Or. 5, 1852, 34–35, p.p.; Warming, Fam. Pod. 6, 1901, 61; Engler, E.P. Nat. Pfl. Fam., ed. 2, 18a, 1930, 32–33, f. 16 A, 24 — *Terniola* Tulasne, Weddell, DC Prodr. 17, 1873, 46–47, p.p.; Bentham

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*) Herba rhizomate repente caulibus filiformibus elongatis ramosissimis. Folia alterna, angustissime linearia, in ramulis floriferis fasciculus subulata basi breviter connata. Flos terminalis. Tepala 3, fere ad usque medium connata. Stamina 3, filamentis filiformibus, antheris 2-loculatis. Ovarium superius, 3-carpellare, 3-loculare, 9-nervatum. Stigmata 3, linearia, libera. Capsula septicide trivalvis. Semina numerosa.

Typus *I. ramosissima* (Wight) van Royen (basion.: *Dalzellia ramosissima* Wight).

& Hooker, Gen. Pl. 3, 1880, 108, p.p.; Hooker, Fl. Br. Ind. 5, 1890, 63, p.p. — *Tulasnea* Wight, l.c., t. 1920, 1 — *Lawia* Tulasne, Warming, E.P. Nat. Pfl. Fam, ed. 1, 3, 2a, 1890, 18, p.p.
Type species. *I. ramosissima* (Wight) van Royen.
Distribution. India.

I. ramosissima (Wight) van Royen, comb. nov. — *Dalzellia ramosissima* Wight, l.c., 1852, 35; Warming, l.c., 1901, 61; Engler, l.c., 1930, 33, f. 16A, 24, as *D. ramosissima* (Wight) Warming — *Terniola ramosissima* (Wight) Weddell, l.c., 1873, 47; Hooker, l.c., 1890, 63 — *Tulasnea ramosissima* Wight, l.c., 1852, t. 1920, 1 — *Lawia ramosissima* (Wight) Warming, l.c., 1890, 18 — *Tristicha ramosissima* (Wight) Willis, Ann. Roy. Bot. Gard. Peradeniya 1, 3, 1902, 208–209 and 1, 4, 1902, 293–306, plates 5–9, 38.
Type specimen. *Johnson s.n.* in K.
Distribution. India.

2. **Terniola** Tulasne, Archives Mus. hist. nat. Paris 6, 1852, 189–194, t. 13; Weddell, DC Prodr. 17, 1873, 46–47, p.p.; Bentham & Hooker, Gen. Pl. 3, 1880, 108, p.p.; Hooker, Fl. Br. Ind. 5, 1890, 62–63 — *Lawia* Tulasne (non Wight = *Adenosachme, Rubiaceae*), Ann. Sc. nat., sér. 3, 11, 1849, 112; Warming, Fam. Pod. 4, 1891, 159–166, 177–178, f. 27–30; Trimen, Fl. Ceylon 3, 1895, 416; Warming, Fam. Pod. 6, 1901, 61; Willis, Ann. Roy. Bot. Gard. Peradeniya 1, 3, 1902, 209–216 and 1, 4, 1902, 307–325, plates 9–13; Engler, E.P. Nat. Pfl. Fam., ed. 2, 18a, 1930, 24, f. 26 — *Mnianthus* Walpers, Ann. Bot. Syst. 3, 1852, 443 — *Tristicha* Gardner, Calc. Journ. of Nat. Hist. 7, 1846, 177 — *Dalzellia* Wight, Ic. Pl. Ind. Or. 5, 1852, 34–35, p.p. — *Tulasnea* Wight, Ic. Pl. Ind. Or. 5, 1852, t. 1919, fgs 1, 3, 4.
Type species. *T. zeylanica* (Gardner) Tul.
Distribution. One species in Ceylon and India.

T. zeylanica (Gardner) Tulasne, l.c., 1852, 190–192, t. 13, f. 3; Weddell, l.c., 1873, 46; Hooker, l.c., 1890, 62; Trimen, Syst. Cat. Ceylon Pl., 1885, 73 — *Tristicha (c)zeylanica* Gardner, l.c., 1846, 177 — *Lawia zeylanica* (Gardner) Tulasne, l.c., 1849, 112; Warming, E.P. Nat. Pfl. Fam., ed. 1, 3, 2a, 1890, 18, p.p.; Warming, l.c., 1891, 177–178, f. 27–30; Trimen, Fl. Ceyl. 3, 1895, 416; Warming, l.c., 1901, 61; Willis, l.c., 1902, 213–216, 307–325, pl. 9–13; Engler, l.c., 1930, 34, f. 21 — *Dalzellia zeylanica* (Gardner) Wight, l.c., 1852, 36; Thwaites, Enum. Pl. Ceyl., 1860, 223 — *Tulasnea zeylanica* (Gardner) Wight, l.c., 1852, t. 1919, 1 — *Mnianthus zeylanicus* (Gardner) Walpers, l.c., 1852, 443 — *Terniola foliosa* (Wight) Weddell, l.c., 1873, 47; Goebel, Pfl. biol. Schild. 1, 1889, 166–170; Warming, l.c., 1901, 61; Engler, l.c., 1930, 34 — *Dalzellia foliosa* Wight, l.c., 1852, 35 — *Tulasnea foliosa* Wight, l.c., 1852, t. 1919, 2 — *Lawia foliosa* (Wight) Warming, l.c., 1891, 159–161, 176–177, f. 26 — *Terniola lawii* (Wight) Weddell, l.c., 1873, 47; Hooker, l.c., 1890, 63 — *Dalzellia lawii* Wight, l.c., 1852, 35 — *Tulasnea lawii* Wight, l.c., 1852, t. 1919, 47 — *Terniola* *longipes* (Tul.) Tul., l.c., 1852, 193–194, t. 13, f. 2; Weddell, l.c., 1873; Hooker, l.c., 1890, 63 — *Lawia longipes* Tul., 1849, 112 — *Mnianthus longipes* (Tul.) Walpers, l.c., 1852, 443 — *Terniola pedunculosa* (Wight) Weddell, l.c., 1870, 47; Hooker, l.c., 1890, 63 — *Dalzellia pedunculosa* Wight, l.c., 1852, 35 — *Tulasnea pedunculosa* Wight, l.c., 1852, t. 1919, f. 4 — *Terniola pulchella* (Tul.) Tul., l.c., 1852, 192–193, t. 13, f. 4; Weddell, l.c., 1873, 46–47; Hooker, l.c., 1890, 62 — *Lawia pulchella* Tul., l.c., 1849, 112 — *Mnianthus pulchellus* (Tul.) Walpers, l.c., 1852, 443.

Type specimen. *Gardner s.n.* in K.

Distribution. India and Ceylon.

Remarks. Willis in 1902 described a number of different forms of this species of which it is doubtful whether they are not only forms of an extremely variable species without deserving the status of a taxonomic form. The nomenclature of these forms, however, will not involve any change of the names given above, and therefore their names are not included here. Future research must reveal their true status.

REFERENCES

BENTHAM, G. & J. D. HOOKER. 1883. Gen. Pl. **3**: 107.

GARDNER, G. July 1846. Calc. Journ. Nat. Hist. **7**: 177–178.

TULASNE, L. R. 1849. Ann. Sc. nat., sér. 3, **11**: 112.

————, 1852. Arch. Mus. hist. nat. Paris **6**: 189–194, t. 13.

WALPERS, G. G. 1852. Ann. Bot. Syst. **3**: 443.

WARMING, E. 1891. Vidensk. Selsk. Skr. 6 Raekke, Afd. **7**, 4: 159–169, 176–179, f. 26–34.

————. 1901. Vidensk. Selsk. Skr. 6 Raekke, Afd. **11**, 1: 61.

WEDDELL, H. A. 1873. DC Prodr. **7**: 46–47.

WIGHT, R. 1852. Ic. Pl. Ind. Or. **5**: 34–35, t. 1919–1920.

WILLIS, J. C. 1902. Ann. Roy. Bot. Garden Peradeniya **1**, 3: 207–216.

————. 1902. Ann. Roy. Bot. Garden Peradeniya **1**, 4: 293–326, pl. 5–13, 38

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A NEW SPECIES OF RHYNCHOLACIS
(PODOSTEMACEAE)

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(*received March* 19*th*, 1959)

In the Podostemaceous material collected by R. E. Schultes and his companions in 1952, one new species in the genus *Rhyncholacis* turned up, characterized by its small size. This species is described below:

Rhyncholacis minima van Royen, n. sp. – *Fig. 1.*

Herba minima, acaulis. Folia repetito-furcata, usque ad 2.5 cm longa; pinnae primariae usque ad 1 cm longae, laciniis ultimis oblongo-spathulatis, enervatis, obtusis vel subacutis. Flos solitarius, pedicello 1.1–2 cm longo. Tepala 5–7, linearia, acuta. Stamina 5–8; anthera obtusa. Ovarium ovoideo-ellipsoideum, 1.5–2.5 × c. 1 × c. 0.7 mm, costis medianis subalatis, costulis aliis indistinctis; styli oblongo-spathulati, c. 0.5 mm longi, basi triangularis in sectio transversi, paulo coherentes. Fructus ovario aequalis, sed costulis distinctioribus.

Small stemless herb up to 2 cm large. Leaves repeatedly forked, up to 2.5 cm long, petiole 4–7 by 0.5–1.5 mm, compressed, widened and sheath-like at base, nerveless, primary pinnae up to 1 cm long, ascending at an angle of c. 55°, ultimate divisions few, oblong-

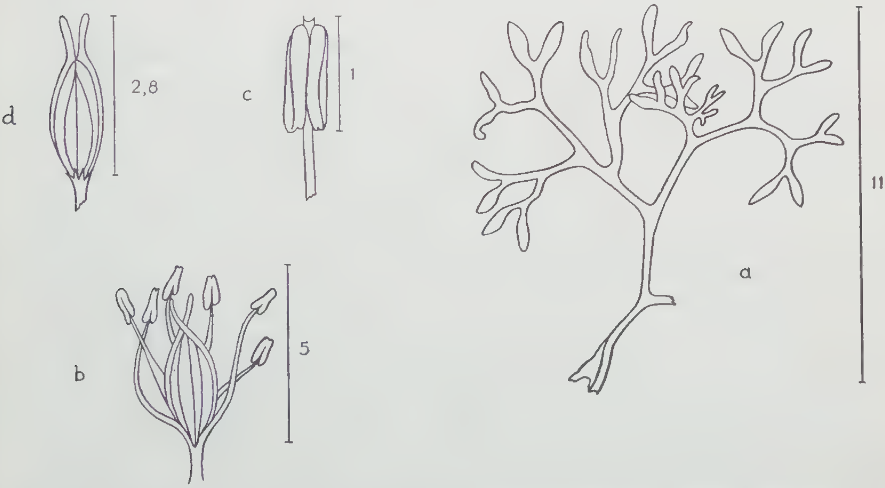

Fig. 1. *Rhyncholacis minima* van Royen; *a:* leaf; *b:* flower; *c:* anther and part of filament; *d:* capsule. (From the type specimen) (L).

spatulate, 1-2 by c. 0.2 mm, obtuse or subacute, nerveless. Flowers solitary, pedicel 1.1–2 cm long, juvenile spathella unknown, mature one tubuliform, 4–6 mm long. Tepals 5–7, linear, c. 0.3 mm long, acute. Stamens 2-tipped, base of thecae rounded. Ovary ovoid-ellipsoid, 1.5–2.5 by c. 0.7 mm, obtuse or rounded at either end, midrib of each carpel only slightly winged, the two other ribs indistinct, styles oblong-spatulate, c. 0.5 mm long, rounded or retuse at apex, 3-sided at base and slightly cohering. Capsule similar to ovary but the ribs more distinct and also the ribs in the margins of the two valves clearer developed.

Type specimen. *Schultes & Baker & Cabrera 18554* in L., dupl. in US.

Distribution. Brazil, prov. Uaupès, Rio Kuduyari, tributary of Rio Uaupès, middle and lower course, Raudal Itapimina, alt. c. 250, fl. and fr. Nov.

Remarks. This species differs from all species in the genus *Rhyncholacis* by its size which is even smaller than that of *R. oligandra* Wedd. and *R. nitelloides* (Wedd.) van Royen. From both species *R. minima* moreover differs in the shorter and broader ultimate divisions of the leaves.

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A SPECIES OF ANTIRHEA (RUBIACEAE) FROM SURINAME

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Antirhea surinamensis Brem. n. spec. ramulis novellis non resinosis, inflorescentiis multifloris, bis ramificatis, floribus 4-meris, ovariis pauciloculаribus ad *A. obtusifoliam* Urb., *A. coriaceam* (Vahl) Urb., *A. Shaferi* Urb., *A. occidentalem* Urb., *A. tenuifoliam* Urb., *A. panamensem* Standl. accedens, sed a speciebus his omnibus ovario et capsula 3-loculari, pedunculis longioribus distinguenda, a speciebus his *A. panamensi* solum excepta insuper foliis acutissime exeuntibus, ab *A. obtusifolia* insuper foliis basi acutis, ab *A. coriacea* inflorescentiae ramulis brevioribus, ab *A. occidentali* et *A. panamensi* corolla extus pilosula diversa.

Habitus nondum accurate notus, sed certe arborescens. *Rami* novelli glabri vel interdum sparse sed longius pilosi, non resinosi, mox cortice griseo-brunneo opaco, plicatulo et sparse lenticellato vestiti, circ. 1.5 mm diam., ex internodiis paucis compositi, internodio infimo 4.5–8.0 cm longo, internodio secundo interdum usque ad 3 cm longo sed plerumque 1 cm haud superante, aliis 0.2–0.6 cm longis. *Folia* petiolata; petiolus canaliculatus appresse pilosus sed ad marginem hirtellus, 3–6 mm longus; lamina elliptica vel obovata, 4.5–10 cm longa et 2.0–4.7 cm lata, apice acuminata et acutissime exeuns, basi acuta, subcoriacea, utrimque opaca, siccitate non conspicue discolorata, supra glabra, subtus costa nervisque densius, inter nervos sparse pubescens, costa supra impressa, subtus prominente, nervis utroque latere costae plerumque 7 prominulis, reticulatione densa siccitate colore saturatiore distinguenda sed haud prominula. *Stipulae* ovato-triangulares, 5 mm longae, extus glabrae, margine tamen ciliolatae, mox deciduae. *Inflorescentia* pedunculo appresse piloso 4.5–7 cm longo instructa; bis pseudo-dichotome ramificata, ramulis primariis 4–5 mm longis, ramulis secundariis 10–15 mm longis, floribus usque ad 12 instructis. *Bracteae* ovato-acuminatae 0.5 mm longae. *Flores* sessiles, ebracteolati, 4-meri. *Ovarium* parce appresse pilosulum, 3-loculare. *Calyx* etiam parce appresse pilosulus tubo 0.2 mm, lobis ovato-triangularibus 0.3 mm longis. *Corolla* extus appresse pilosula, tubo 7–8 mm longo et 0.8 mm diam., intus glabro, lobis elliptico-orbicularibus 1.4 mm longis et 1.0 mm latis. *Stamina* filamento brevissimo instructa; antherae dorsifixae fere 0.5 mm infra orem tubi inclusae, lineares, 2.6 mm longae. *Granula pollinis* 3-pora, distincte reticulata, 25 μ diam. *Discus* cylindricus 0.4 mm altus. *Stylus* glaber,

tubo aequilongus; stigma capitatum. *Drupa* glabra, 9 mm alta et 4.5 mm diam., pyrena 3-lobata et 3-loculari.

Habitat Guyanam Batavorum.

Suriname: region of the Maratakka River, Helstone 237 U, type, 6.6.1958.

This species shows no near affinity with *A. guianensis* Brem. (Kew Bull. 1952: 260) from British Guiana, the only other representative of this genus that is known so far from the South American continent, but it comes perhaps nearest to *A. panamensis* Standl., from which it differs in the slightly shorter petioles, the somewhat wider and larger leafblade, the longer peduncle, the outside pilosulous corolla and the 3-celled ovary. *A. panamensis* belongs, like the other species mentioned in the diagnosis to a group with non-resinous branches, many-flowered inflorescences and ovaries with two or three cells, whereas *A. guianensis* forms part of a group of species with resinous branches, few-flowered inflorescences and ovaries with at least four cells. The differences between these two groups are probably even more pronounced, for in the species of the first group of which flowers were available to me, the style proved to be as long as the corolla tube and to end in a capitate stigma, whereas in the species of the other group, it is less than half as long as the tube, and it goes out into linear stigmata. This means that the flowers of the second group are provided with the same pollination mechanism that I described for *Kohautia* DC, the subgenus *Eusipanea* K. Sch. of *Sipanea* Aubl., *Cladoceras* Brem. and *Posoqueria* Aubl., but which occurs also in species of the nearly related genera *Guettarda* L and *Laugeria* Vahl (see my work on "the African species of Oldenlandia L sensu Hiern et K. Schumann" in Verh. Kon. Ned. Akad. v. Wetensch., Afd. Natuurk. 2nd Ser., Vol. **48**, No. 4, 1952, p. 27 and 28). There seems also to be a difference in pollen structure, for although they are everywhere globose and 3-porous, they are in the two species of the first group which I could study, viz. *A. surinamensis* and *A. lucida* (DC) Bth. et Hook. f., very distinctly reticulate, whereas in the two species of the second group from which they are known to me, viz. *A. guianensis* and *A. acutata* (DC) Urb. they are either smooth or minutely punctate. These features should, of course, be studied in a far larger number of species, but it is not improbable that such a study will lead to a splitting of the genus. However, before such a step can be taken, the Old-World species should be studied too. Of the latter no good material was available to me, and the only thing I can say at the moment is that the species from the Malay Archipelago differ from the American ones in the peculiar design of the leaves, which is the same as that seen e.g. in the genera *Sommera* Schlecht. and *Pentagonia* Bth., and which is usually referred to as moiré or watered striation.

The branches of *A. surinamensis* show the sympodial structure which I have described years ago from *Terminalia*, *Elaeocarpus* and some *Sapotaceae* (De Tropische Natuur **25**: 9. 1936). They start with a long internode, which is followed by some rather short ones; then further elongation stops. Growth is resumed by one or two axillary branches arising from the axil of one or two of the leaves belonging to the short internodes. Sympodial branches of this type are also met with in *A. lucida* and in *A. obtusifolia*, but it is certainly no general feature of the genus, not even of the first group.

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A NEW STAUROGYNE FROM THE TERRITORY OF PAPUA

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(*Botanical Museum and Herbarium, Utrecht*)

(*received March 20th*, 1959)

The new species described below belongs like *St. leptocaulis* Brem. (in Nova Guinea, new ser., 8: 129. 1957) to the subgenus *Tetrastichum*, which is characterized by the presence in each of the ovary cells of circ. 60 ovules arranged in four rows and by the lower flowers of the inflorescence being subtended by ordinary leaves. The new species is easily distinguishable from *St. leptocaulis* by its larger and relatively wider leaves and by its obovate-orbicular bracts.

Staurogyne latibracteata Brem. n. spec. ad subgenus *Tetrastichum* pertinens, caule ascendente et antheris appendiculatis ad *St. Neesii* (Vidal) C. B. Clarke ex Merr., *St. rivularem* Merr. et *St. leptocaulem* Brem. accedens, caule pilis capitatis vestito praesertim *St. Neesii* et *St. leptocauli* similor sed bracteis multo latioribus ab eis et a speciebus omnibus huius generis hactenus notis faciliter distinguenda.

Herba e basi decumbente ascendens, 18–25 cm alta, parce ramosa, sine brachyblastis sterilibus. Caulis pilis pro parte capitatis satis dense vestitus, in parte decumbente 2 mm diam., in parte ascendente circ. 1 mm diam., internodiis circ. 1.5 cm longis. Folia fere omnia opposita, sensim in petiolum subtus pubescentem usque ad 1 cm longum contracta; lamina lanceolato-oblonga vel oblanceolata, 4.5–8.0 cm longa et 1.8–2.5 cm lata, apice obtusa, basi cuneata vel contracta, discolor, sicc. supra olivacea, subtus griseo-viridis, primum supra sparse strigosa sed mox glabrescens, subtus primum pilis capitatis dense pubescens, deinde costa parce pubescente excepta etiam glabrescens, nervis utroque latere costae 5–7. Inflorescentia caulem terminans interdum inflorescentiis aliquibus ramos longiores terminantibus comitata, spiciformis. Folia flores inferiores suffulcientes gradatim magnitudine decrescentia, apice obtusissima; bracteae florum aliorum obovato-orbiculares, 5.5–9.0 mm longae et 4.0–8.0 mm latae, mucronatae, pilis capitatis utrimque sed ad marginem densius pubescentes, utroque latere costae plerumque nervis 2 instructae. Bracteolae lineares, 5 mm longae et 1.2 mm latae, acutae, pilis capitatis densius pubescentes, 1-nerviae. Calycis lobus posticus lineari-oblongus 7 mm longus et 2 mm latus, acutus, 3-nervius; lobi antici lineares 5 mm longi et 0.2 mm lati; lobi laterales filiformes 3.5 mm longi; omnes pilis capitatis pubescentes. Corolla dilute purpurea lineis purpureis striata 11 mm longa, extus glabra. Stamina thecis basi vix notabile appendiculatis instructa. Staminodium ecapitatum 2 mm longum. Ovarium glabrum. Capsula glabra 5 mm longa.

Territory of Papua: Milne Bay District, near Guru village (North coast of Cape Vogel Peninsula), alt. 10 m, R. D. Hoogland 4740 CANB, type, dupl. L, LAE.

The affinity with *St. Neesii* (Vidal) C. B. Clarke ex Merr., *St. rivularis* Merr. and *St. leptocaulis* Brem. is doubtless more pronounced than that with the species occurring in the western part of the area. It manifests itself in the ascendent stem and in the appendiculate anthers. *St. latibracteata* differs from these three species in the absence of brachyblasts in the axils of the leaves, the much greater width of the bracts and the broad posticus calyx lobe.

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A KEY TO THE SPECIES OF HALOPHILA (HYDROCHARITACEAE), WITH DESCRIPTIONS OF THE AMERICAN SPECIES

C. DEN HARTOG

(*Foundation Flora Malesiana, Leyden*)

(*received March* 31*st*, 1959)

During the revision of the Hydrocharitaceous genus *Halophila* for the Flora Malesiana it appeared for nomenclatural reasons necessary to study the genus in its entirety. In this Flora (Den Hartog, 1957b) I have already accounted for the Malaysian species. In that paper I have also included *H. stipulacea* (Forsk.) Aschers. which is commonly distributed in the western part of the Indian Ocean and the Red Sea and has immigrated in recent years via the Suez Canal into the eastern Mediterranean. A new species, *H. linearis* Hartog, I have described (Den Hartog, 1957a) from Portuguese East Africa. The remaining American species, all occurring in the Caribbean, will be treated in this paper. In order to facilitate the study of this interesting marine genus a key to all species has been prepared.

Key to the species

1. Lateral shoots with 2 scales at the base.
   2. Lateral shoots with at the top at most 5 pairs of petioled leaves.
      3. Lateral shoots short, 1 cm or smaller, often not developed with 1 pair of leaves at the top; petioles not or unequal-sided sheathing . . . . sect. HALOPHILA
         4. Midrib joining the intramarginal nerves; cross-veins present.
            5. Scales to 8 mm; leaves ovate or elliptic; petiole not sheathing.
               6. Lateral shoots scarcely or not developed; glabrous, margin entire, dioecious.
                  7. Leaves 1–4 cm, with 12–25 pairs of cross-veins ascending at an angle of 45–60°. 1. **H. ovalis** (R.Br.) Hook. f.
                  7. Leaves 0.7–1.4 cm, with 3–8 pairs of cross-veins, ascending at an angle of 70–90°. 2. **H. minor** (Zoll.) Hartog
               6. Lateral shoots 0.5–10 mm; hairy, margin serrulate, monoecious . . . 3. **H. decipiens** Ostenf.
            5. Scales large, 12–17 mm, bright white, leaves linear; petioles unequal-sided sheathing. 4. **H. stipulacea** (Forsk.) Aschers.

4. Midrib joining the marginal nerves in the top, cross-veins absent . . . . 5. **H. linearis** Hartog

3. Lateral shoots longer, 1–2 cm, with 6–10 leaves at the top; petioles with a broad sheath; midrib crossing the intramarginal nerve, reaching the margin; cross-veins absent. sect. MICROHALOPHILA Aschers . . 6. **H. beccarii** Aschers.

2. Lateral shoots with 10–20 pairs of sessile, distichous leaves. sect. ASCHERSONIA Hartog. . 7. **H. spinulosa** (R.Br.) Aschers.

1. Lateral shoots with 2 basal scales and 2 others halfway up or higher, at the top 2 or 3 pairs of leaves, placed in a pseudo-whorl. sect. AMERICANAE (Ostenf.) Ostenf.

8. Leaves distinctly petioled, obtuse, with 3–5 pairs of cross-veins; petioles 3–5 mm . . . . 8. **H. baillonis** Aschers.

8. Leaves subsessile or very shortly petioled, acute, with 6–8 pairs of cross-veins . . . . 9. **H. engelmanni** Aschers.

SECT. HALOPHILA. — sect. *Barkania* (Ehrenb.) Aschers. Nuov. Giorn. Bot. Ital. **3**: 301. 1871; Hartog, Act. Bot. Neerl. **6**: 46. 1957; *Typicae* Ostenf. Bot. Tidsskr. **24**: 240. 1902; Pfl.-areale **1**^{3}: 37. 1927.

Lateral shoots short, 1 cm or smaller, often not developed, with only 1 pair of leaves at the top.

Halophila decipiens Ostenf. Bot. Tidsskr. **24**: 260 fig. 1902; Aschers. in Neumayer, Anl. Wiss. Beob. Reisen ed. 3, **2**: 395. 1906; Gagnep. Fl. Gén. I.-C. **6**, 1: 4. 1908; Ostenf. Pfl.-areale **1**^{3}: 37, 38, map 23. 1927; Steenis, Trop. Natuur **22**: 46. 1933; Setchell, Am. Naturalist **69**: f. 3. 1935; Hartog, Fl. Mal. **5**: 410 f. 18. 1957. — *H. baillonis* (non Aschers. 1874) Aschers. in Neumayer, Anl. Wiss. Beob. Reisen ed. **1**: 367. 1875; d'Eggers, Smiths. Inst. Bull. Nat. Hist. **13**: 98. 1879 (*baillonii*); Holm, Bih. K. Svenska Vet.-Ak. Handl. **9**, 13: 1–18, pl. 1–3. 1885; Aschers. & Gürke in E. & P. Nat. Pfl. fam. **2**, 1: 249. 1889; Aschers. in Neumayer, Anl. Wiss. Beob. Reisen ed. 3, **2**: 395. 1906; Rydberg, N. Amer. Fl. **17**: 67. 1909; Bowman, Science **43**: 245. 1916; Pap. Michigan Ac. Sc. Arts & Lett. **2**: 5, pl. 2. 1922; Ostenf. Pfl.-areale **1**^{3}: 37, 38 map 23. 1927; Setchell, Am. Naturalist **69**: f. 3. 1935.

After the character of the indument of the leaves and the spathal leaves two varieties can be distinguished. The var. *decipiens* has hairs on one side of the leaf only and glabrous spathal leaves. The var. *pubescens*, however, has the leaves hairy on both sides, and the spathal leaves with hairy outer side.

var. **pubescens** Hartog, Fl. Mal. **5**: 411. 1957.

Monoecious. Stems thin, easily breaking, with one root at the nodes, internodes 1–4½ cm. Scales transparent, scarious, obovate, doubled, keeled, 3–7 mm, outerside hairy, apex incised. base amplexicaulous. Leaves oblong-elliptic, obtuse or rounded, cuneate at the base, green, at both sides faintly covered with short, rigid, unicellular hairs, margine very fine-serrulate, 10–23 by 3–6 mm, only 1 pair on a 1–10 mm long shoot; cross-nerves 6-9 pairs, ascending, joining the intramarginal nerve; midrib united at the top with the intramarginal nerves running at c. 5 mm distance from the margin; petiole 3-15 mm, triquetrous. Spathe ovate, acuminate, keeled, scarious, transparent, 3–4 mm, margin ciliate and keel with fine serrulate teeth, hairy outside, tearing at the top as the fruit is ripening, containing 1 ♂ and 1 ♀ flower, spathe leaf enclosing the female flower, embracing the other. Male flower: tepals oblong-elliptic to ovate, obtuse, convex, 1–1 ½ mm long, anthers c. 1 mm, pollen grains elliptic; pedicel 3 mm; after anthesis the complete flower with its pedicel caducous. Female flower subsessile, ovary ovate, 1 mm; beak 1–2 mm; styles 3, 2 ½ mm. Fruit broad-elliptic, 2 ½ by 1 ½ mm; pericarp scarious, transparent, beak 1 ½–2 mm. Seeds c. 30, ovate, 1/5 mm.

Distribution: West Indies (Porto Rico, Jamaica, Guadeloupe, Martinique, St Thomas, St Croix); Florida. Also with great disjunctions in the Indo-Pacific: Tahiti, Ceylon.

The closely related var. *decipiens* occurs very localized in a few stations, but widely distributed in the Indo-Pacific.

Ecology: On muddy bottoms and on coarse coral sand, from 1–50 m depth; in shallow water sometimes associated with *H. baillonis*, in deep water sometimes together with *H. engelmanni*. Fl. and fr. probably the whole year round.

Material studied:

CARIBBEAN: Martinique, L. Hahn 1271, Plante marine, mer de la Casi-Pilatz. Nov. 1849 (P); St Croix, Christiansted Lagoon, Ostenfeld 290, 9 Febr. 1914 (C); Porto Rico, Margarita Pass, near Parguera, dredged in 18–20 m of water between outer reefs, Howe 7219, 27 June 1915 (P); Island of Culebra Harbor, Howe, 3–12 March 1906 (K); Florida, 10 fms, 18–20 fms, without other data (BM).

INDO-PACIFIC: Tahiti, Papeete Harbour, Challenger Expedition, Moseley, Sept. 1875 (BM, K); at 18 m, 15 Oct. 1928 (C, L); Páea, 5 ft deep near head of deep channel, Crossland 7149, 26 Jan. 1929 (K); Ceylon, Chilam, in 6 fms, Nevill 1484, April 1881 (K).

Nomenclature: Difficulties around the name *H. baillonis* are exclusively due to Ascherson, whose imperfect description applies to 2 species. The name had been used for the first time by him in a letter to Prof. Oliver, about a *Halophila* species, collected by Moseley during the Challenger Expedition at St Croix. In this letter, published by Hooker f. in 1874, Ascherson stated that *H. baillonis* differs from *H. ovalis* by the serrulate leaves. Further he communicated the species had previously also been collected by Hahn in Martinique. I have seen the Challenger material which has been kept together with Ascherson's letter in the Kew Herbarium and I consider this material to represent the type specimen of *H. baillonis*. It has 2 scales halfway or higher on the lateral shoot, and at the top a pseudowhorl of 4 shortly petioled leaves.

The specimens collected by Hahn, in 1874 erroneously referred to *H. baillonis* by Ascherson, which I have examined, have also a very fine serrulate leaf margin but they belong to *H. decipiens*. In his material the lateral shoots are very short, bear no scales and have at the top only 1 pair of rather long-petioled leaves. Fortunately Ascherson did not cite the Challenger St Croix material in his paper of 1875, and mentioned only localities where *H. decipiens* had been found. The very detailed descriptions of d'Eggers and of Holm also concern this

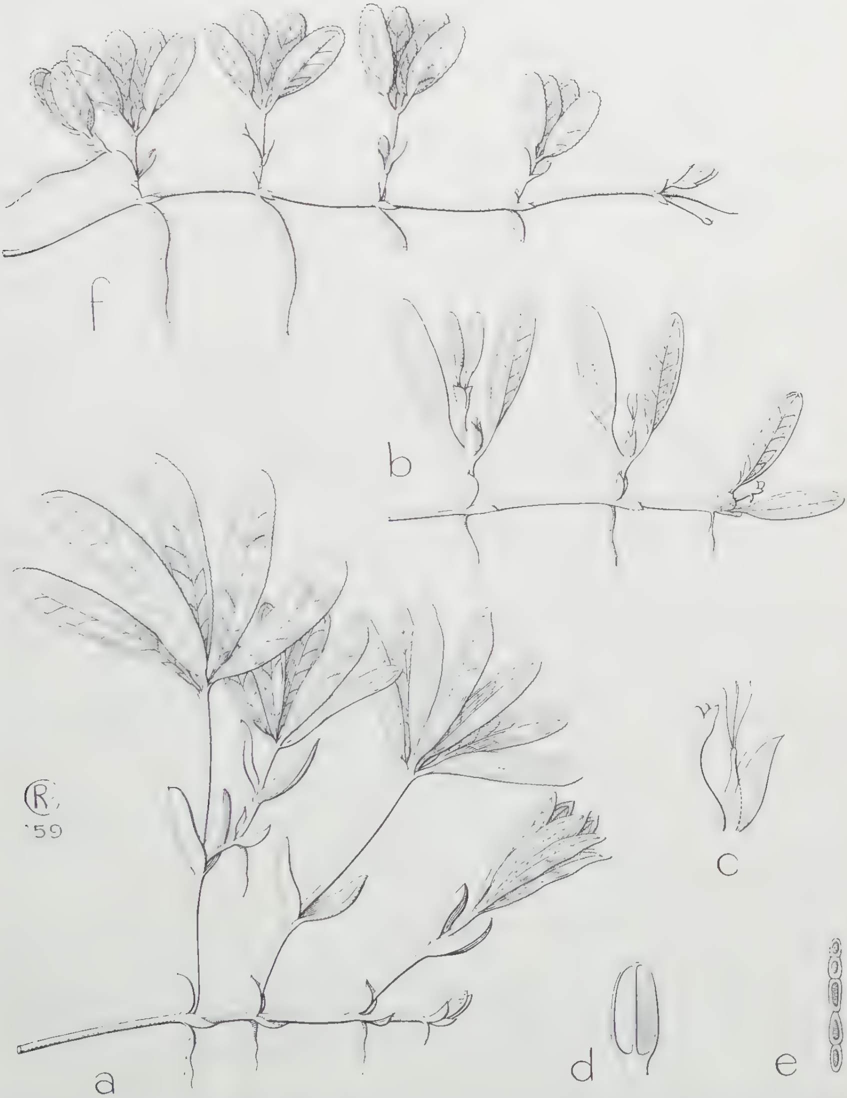

Fig. 1. a. *Halophila engelmanni* Aschers., habit, nat. size. b. *H. decipiens* Ostenf., habit, nat. size, c. flowers, d. lengthwise section of anther, e. part of pollen thread, enlarged. f. *H. baillonis* Aschers., habit, nat. size (a Curtiss 2704 in L, b–f after Ostenfeld, 1902).

species. Thanks to the excellent illustrations of Holm, all subsequent authors identified it wrongly as *H. baillonis*. Recently (DEN HARTOG 1957b) I merged both species (i.e. *H. baillonis* auct. and *H. decipiens*), because the differences are very slight and show no geographic separation.

SECT. AMERICANAE (Ostenf.) Ostenf. Pfl.-areale **1**³: 37. 1927; Bot. Tidsskr. **24**: 240. 1902; Hartog, Fl. Mal. **5**: 408. 1957.

Lateral shoot halfway or higher up with 2 scales and at the top 2 or 3 pairs of pseudoverticillate leaves.

Halophila engelmanni Aschers. in Neumayer, Anl. Wiss. Beob. Reisen ed. **1**: 368. 1875; Bth. & Hook. f. Gen. Pl. **3**: 455. 1883; Aschers. in Neumayer, Anl. Wiss. Beob. Reisen ed. 3, **2**: 395. 1906; Rydberg, N. Amer. Fl. **17**: 68. 1909; Bowman, Science **43**: 245. 1916; Pap. Mich. Ac. Sc. Arts & Lett. **2**: pl. 1. 1922; Ostenf. Pfl.-areale **1**³: 37, 38 map 24. 1927; Setchell, Am. Naturalist **69**: f. 4. 1935; Hartog, Fl. Mal. **5**: 408. 1957.

Dioecious. Stems thin, easily breaking, at the nodes one root; internodes 2–4 cm. Scales at the base of the lateral shoots broadly obovate, transparent, scarious, glabrous, keeled; apex obtuse, sometimes a little incised, margin entire, 3–6 mm long. Lateral shoots 2–4 cm, at the middle with 2 lanceolate to obovate scales, 4–12 by 1–3 mm, at the top with 2–4 pairs of leaves in a pseudowhorl. Leaves oblong or linear-oblong, glabrous, apex obtuse, sometimes apiculate, base cuneate; margin finely serrate; 10–30 by 3–6 mm, rather thick. On either side of the midrib 6–8 cross-nerves, ascending under an angle of 30–45°, joining the intramarginal nerve. Midrib united at the top with the intramarginal nerves. Petiole: 2 mm or shorter. Spathe-leaves lanceolate, acuminate, sessile in the axils of the leaves, containing 1 female flower. Ovary ovate, 3–4 mm; rostrum 5 mm long; styles 3, 3 cm long. (Description of the flower after Rydberg, l.c.) Male flower unknown.

Distribution: Florida and Bahama Islands.

Ecology: On fine white sediments of limy remainder of echinoderms, mollusca, corals, in clear water on a depth to 16–18 fathoms, associated with a lot of algae (*Halimeda*, *Caulerpa*, *Codium*, *Udotea*, etc.), sometimes also with *H. baillonis* var. *pubescens*.

Material studied:

FLORIDA: Cape Sable, washed up with algae. Also found at Cedar Keys, Punta Rossa, and in the Indian River, Curtiss 2704, Jan. (K, L); Punta Rossa, thrown up with algae, Curtiss, July 1881 (P); Lake Worth, growing with marine algae, Curtiss 5399, 22 May 1895 (K); Key West, W. H. Hervey (K).

Halophila baillonis Aschers. ex Hook. f. Journ. Linn. Soc. **14**: 317. 1874; Bth. & Hook. f. Gen. Pl. **3**: 455. 1883; Hartog, Fl. Mal. **5**: 408. 1957. — *H. aschersonii* Ostenf. Bot. Tidsskr. **24**: 239, fig. 1902; Aschers. in Neumayer, Anl. Wiss. Beob. Reisen ed. **3**, 2: 395. 1906;

Rydberg, N. Amer. Fl. **17**: 68. 1909; Ostenf. Pfl.-areale **1**^{3}: 37, 38 map 24. 1927; Setchell, Rev. Sudamer. Bot. **1**: 107. 1934; Am. Naturalist **69**: f. 4. 1935.

Dioecious. Stems thin, easily breaking, at the nodes one root; internodes 1–3 cm. Scales at the base of the lateral shoots lanceolate to obovate, transparent, scarious, pubescent, keeled, 1–2½ mm; apex obtuse, sometimes a little incised; margin entire. Lateral shoots 6–40 mm, with halfway or higher 2 obovate scales, 3–4 mm in the axils of which often arise secundary shoots, and at the top with 2 pairs of leaves, placed in a pseudowhorl. Leaves oblong, elliptic to lanceolate, hispidulous; apex obtuse, base cuneate; margin finely dentate; 5–20 by 2–8 mm. On either side of the midrib 3–5 cross-nerves, ascending under an angle of 60–80°, joining the intramarginal nerve. Midrib united at the top with the intramarginal nerves. Petiole 3-5 mm. Spathe-leaves lanceolate, acute, sessile in the axils of the upper pairs of leaves, containing one female flower. Ovary ovate, 2 mm; rostrum slender, 5 mm; styles 2 or 3, 15–30 mm long, with rather conspicuous papillae. (Description of the flower after Rydberg, l.c.) Male flower unknown.

Distribution: West Indies (Porto Rico, Jamaica, St Croix). Brasil: Pernambuco. Setchell l.c. assumes that the specimens collected in Brasil are not autochthonous.

Ecology: Muddy bottoms of bays at a depth of about 1 m, sometimes together with *H. decipiens* var. *pubescens*.

Material studied:

CARIBBEAN: St Croix, Challenger Expedition, Moseley, 1873, type (K); Christiansted, F. Børgesen, Jan. 1906 (BM); Curaçao, Spaanse water bij Brakke Punt, P. J. van Breemen, 1913 (U).

BRASIL: Pernambuco, on mud, G. A. Ramage, 1887 (BM).

REFERENCES

HARTOG, C. DEN. 1957a. Act. Bot. Neerl. **6**: 46, fig.
————. 1957b. Fl. Mal. I, **5**: 407–413, fig. 16–19.

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BRIEF REPORTS

WENT, Johanna C.: Cellophane as a Medium to study the Cellulose Decomposition in Forest Soils

Richard (1945) described a method to test the cellulose and protein breakdown in the soil. He placed viscose and silk threads in the soil sometimes for more than one year and measured their tensile strength after removal from the soil.

This method was used by Van Goor (1952) for forests soils in the Netherlands. He measured the tensile strength of rayoncord A U, a twisted cellulose thread, while Hueck (verbal information) measured the tensile strength of a cylindrical non twisted cellulose thread. Measuring the tensile strength has to be done under constant temperature and humidity and it is not easy to get reproducible results.

I have tried therefore to use the non twisted thread [1] (a cylindrical isotropic regenerated cellulose thread), which can be cleaned better after removal from the soil than the twisted one. The threads are weighed before and after their treatment. Results, however, were confusing as many threads were partly eaten by soil animals and often it was impossible to recover the entire length from the soil. Since the cellulose threads did not give reproducible results the time necessary for the disappearance of the cellophane in the soil is now used as a criterion for the decomposition of cellulose in the soil.

Accidentely cellophane was used in this way when the method of Tribe (1957) to study the invasion of cellophane by soil organisms was repeated. The cellophane is folded around a microscope slide and kept around this slide with a second slide, fastened together on one end with adhesive tape. The unvarnished cellophane is boiled before use to get rid of the plasticizers in this material. The slides were placed vertically in the soil and the development of fungi and bacteria was followed at intervals of one to two weeks. Already after one week the cellophane is invaded by fungi and bacteria. After two weeks an etching of the cellophane underneath the fungi and bacteria could be seen. Many fungi formed a fanshaped growth on the cellophane. Especially under the fanshaped growth the cellophane was attacked and small holes appeared. When all the cellophane is invaded by fungi, mites and springtails will start to eat holes in the moldy cellophane until it has disappeared entirely. The only animals attacking the cellophane before it is invaded by fungi and bacteria are snails or slugs. It may be mentioned that these animals have cellulase in their digestive tract.

It is not possible to recognize the fungi when they are growing on cellophane. Therefore isolates were made from the newly invaded cellophane and pure cultures of the isolated organisms were grown on cellophane placed on an agar layer with only inorganic salts as nutrients. In this way it was found that *Staphylotrichum*, described by Nicot and Meyer (1956) from a tropical soil, formed a fanshaped growth which was very similar to a chytridiacea, *Rhyzophlictis*. This shows how confusing the growth on cellophane can be. *Staphylotrichum* digests the cellophane at a temperature of 10° C in 3.5 weeks. *Myrothecium*, a well known cellulose attacking fungus digests the cellophane in less than 7.5 weeks. Both *Myrothecium* and *Staphylotrichum* were isolated from the Hackfort oakforest soil.

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[1] The non twisted cellulose thread was obtained from the Centraal Laboratorium, Delft and from the AKU, Arnhem. The last also procured the cellophane.

As the disappearance of the cellophane is much slower in forest soils than when used for the growth of pure fungus cultures at the same temperatures, it is evident that antagonistic action of different organisms or other influences of the environment slows down the digestion of the cellophane.

In 4 different forest soils, calcareous mull, acid mull, and mor from Hackfort oakforest and acid mull from Middachten oakforest, the rate of decomposition of cellophane was investigated (table I). The Hackfort soil is a sandy soil mixed with loam, the Middachten soil is a clay soil. Not the pH, but probably the moisture content is one of the most important factors for the breakdown of the cellophane in these different forest types. The Middachten acid mull which decomposes quickly is very wet, the Hackfort mor which has the same acidity is a much drier soil with much slower decomposition.

TABLE I

Number of weeks necessary for the disappearance of cellophane in different forestsoil types

Oakforest	Condition of the soil	pH (KCL)	pH (water)	Weeks
Hackfort	calcareous mull	5.2	5.9	12–23
Hackfort	acid mull	3.4	4.3	26–39
Hackfort	mor	3.0	4.1	20–45
Middachten	acid mull	2.8	4.1	7–10

As temperature and moisture condition of the soil are important factors in the decomposition it is obvious that the time of disappearance will show great variation in different periods of the year.

In 1953, squares in a pine forest on sandy soil, were treated in 3 different ways. One part was dug to a depth of 20 cm. The other two parts were dug in the same way but one part was treated with ground lime marl (2000 kg pro ha) and the other part with hydrated lime (1950 kg pro ha). Now after 6 years the cellophane shows a marked difference in disappearing. Little or no disappearence could be found in the parts that were dug and treated with hydrated lime after 18.5 weeks. The untreated part showed some breakdown after 11 weeks and an appreciable breakdown after 14.5 weeks. The part treated with ground lime marl showed even more breakdown after 14.5 weeks than the untreated part. It might be possible that an initial heavy breakdown in the part that is dug or treated with hydrated lime may have caused the absence of breakdown later on. The experiment will have to be repeated with freshly treated soil.

These experiments show the possibilities of cellophane as an indicator of cellulose decomposition in the soil.

REFERENCES

Goor, C. P. van. 1952. T.N.O. Nieuws **7**: 11.
Nicot, Mrs J. and J. Meyer. 1956. Bull. Soc. Myc. France **72**: 4.
Richard, F. 1945. Mitt. Schweiz. Anst. Forstl. Versuchsw. **24**: 297.
Tribe, H. T. 1957. Microbial Ecology, 7th Symp. Soc. Gen. Microb.: 287.

BOOK REVIEWS

OF PUBLICATIONS RELATED TO BOTANICAL WORK IN THE NETHERLANDS

Audus, L. J.: Plant growth substances, Leonard Hill (Books) Ltd. London, 1959. Price 65/-. 576 pages, 58 illustrations. Size 10″ × 6″. (Royal 8vo).

This second edition of "Plant Growth Substances" is the first book of a new series entitled "Plant Science Monographs". The series, of which another twelve titles have been announced already, is designed to facilitate the effective application of research in the plant sciences and, as a result of this, the improvement of productivity. In order to present the physiological background of the use of growth-regulating substances in agriculture and horticulture to the layman and the non-specialist, the treatment has been kept as simple as is consistent with accuracy. Some two or three Chapters, nevertheless, will probably be beyond the comprehension of the non-scientific layman. They deal with the nature of plant growth and its control, with the chemistry of the natural and synthetic auxins and with their mode of action in the plant cell. In the remaining Chapters every practical aspect of growth-substance application is covered: auxins as growth stimulants, as initiators of new organs, the use of auxins in grafting and wound healing, the initiation and stimulation of fruit development, the control of the shedding of various parts, the action of auxins as growth inhibitors (bud growth and induced dormancy, general toxicity and use as selective weed killers). The last Chapters deal with the role played by hormones in reproduction, with the calines, with natural plant-growth inhibitors and with the growth substances in the soil. An extensive glossary, five appendices and over a thousand references complete the book. The reader is led through these parts of the domain of plant physiology in an extremely attractive way. Professor Audus is a guide who has not only a keen interest in the history of the existing scientific structures, he is also a good judge of the possibilities and the difficulties of those constructions which are not yet fully established. He has assimilated the large quantity of physiological data so efficiently that the structures formed with them, constituting the Chpaters of the book, are each of them extraordinary examples of integration. Moreover, the book is pleasant reading. To anyone interested in plant physiology and in the application of chemicals to plant-growth control "Plant Growth Substances" will be of great value. — Professor Audus stayed a few years in the erstwhile Netherlands East Indies, not as a scientific worker in an Experiment Station but as a prisoner-of-war in a Japanese camp. Since the food was inadequate, serious symptoms of vitamin deficiency spread among the inhabitants. Prof. A. developed in his camp methods to grow yeast, and it is not improbable that many of his companions owe their life to his ability to apply his broad knowledge of general botany on problems of food production, even in the worst circumstances imaginable. L. A.

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NUTRIENTS IN THE GIANT EMBRYOSAC–VACUOLE OF THE COCONUT

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(*received June 23rd, 1959*)

INTRODUCTION

The large vacuole in the embryosac of the coconut makes it possible to analyse vacuole sap without admixture of protoplasmatic substances, and thus to find out what nutrients are present or lacking. This vacuole is probably the second largest in plants. Another palm, *Loidoicea Seychellarum*, has still larger nuts.

The analyses were carried out by Mr. A. C. Spoelstra and Mr. H. J. Immink under supervision of Dr. W. B. Deys of the Institute for Chemical and Biological Research on Field Crops at Wageningen. Amino acids were determined by Dr. J. van Die of the Laboratory for Plant Physiology, also at Wageningen. Samples of the sap and leaves were taken by Ir. H. Hoestra at Togo. The author is much indebted to these gentlemen for their kind help.

MATERIAL AND METHODS

On a fullgrown coconut a new leaf appears every four weeks. In the axle of each leaf a spadix develops with male and female flowers. After opening of the spadix the male flowers bloom first and then the female flowers are open at the time when the spadix of the next leaf opens. The inflorescence with flowers develops into a bunch of nuts, the successive bunches thus having difference in age of about four weeks.

The female flower of the coconut palm contains three ovules, one to each carpel. Of these only one develops after pollination. The embryosac of this ovule increases enormously in size and becomes the large cavity filled with sap in the nut. The final size is attained about six months after opening of the spadix (Fig. 5) and a nut may then contain more than half a litre of sap. At this time the formation of endosperm starts and can first be observed as a small jellylike patch on the apex of the cavity. At the base of the cavity the embryo will form (Figs. 1–4). As long as no endosperm is formed the cavity is the vacuole of the single large embryosac cell. The liquid is under pressure and a little sap spouts out when a hole is made in the wall, e.g. for drinking coconut water. When the endosperm is formed the pressure disappears gradually and a gasbubble is formed in the end. The liquid then thumps when the nut is shaked. Samples were taken from nuts of the oldest bunch where no endosperm could be found (Fig. 2). These samples were taken at Togo, preserved with a little toluene and sent to Europe.

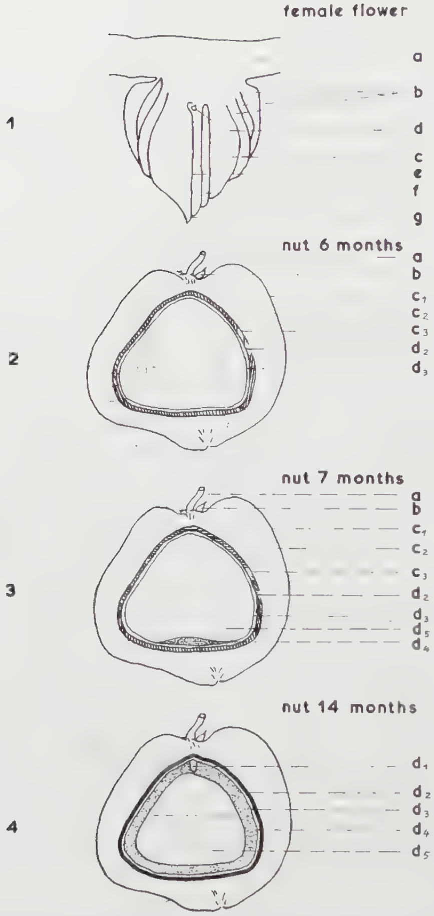

Fig. 1. Female flower; Figs. 2 and 3. Unripe nuts; Fig. 4. Ripe nut of the coconut palm. Samples of fluid were taken from stage 2, that is about 6 months after opening of the spadix. a. stalk; b. perianth; c. gynoecium in flower and in fruit: c_1 exocarp, c_2 mesocarp (husk), c_3 stony layer of endocarp (shell.); d. ovule in flower and in fruit: d_1 embryo, d_2 and d_3 outer and inner seed coats, d_4 endosperm (coconut meat), d_5 cavity filled with fluid, in ripe nuts only partly filled; e. conductive channel; f. nectarium; g. stigma.

Samples, analysed by other authors, are from sap of ripe nuts and may therefore differ from the above mentioned samples (SALGADO, 1954). Such samples being intended for other purposes cannot give an impression of the vacuole sap, as in the later stages the character as a vacuole is lost.

For comparison of the analysis of the sap, leaf samples were taken, according to the method described by PRÉVOT (1954) for oil palms. This was done by taking the first fully developed leaf and from it a sample from the middle leaflets and the centre part of each of these leaflets. The leaves were oven dried, but wet weight was calculated on a basis of 75 % water.

The identification of the pure amino acids present, and the estimate of the amount of total amino and amide Nitrogen in the leaves was performed on fresh material, sent by airmail.

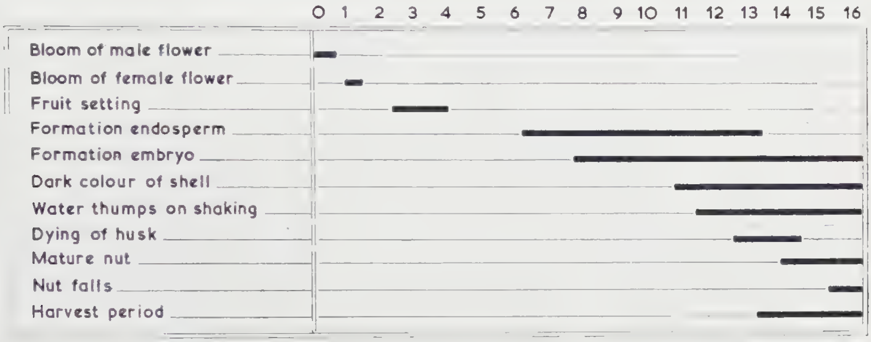

Fig. 5. Development of the fruit of the Coconut palm. On horizontal axis the time in months (after Tammes 1940).

Macronutrients

The sap from the vacuole contains about 2 % of monoses and a trace of sucrose. The sap is under pressure. Ph is about 5.8. The following nutrients were found (Table I).

Table I

	Tree	Macronutrients in mg/l in sap or mg/kg in leaves					
		N	N.amino acids	P	K	Ca	Mg
sap	T 6	90	78	58	3050	288	47
	T 8	73	31	59	2730	289	48
fresh	T 6	5825	—	280	3125	785	315
leaf	T 8	5280	—	270	1425	1040	312
dry	T 6	23300	—	1120	12500	3140	1260
leaf	T 8	21400		1080	5700	4160	1250

Nitrogen. Only 2 % of the total amount of nitrogen in the leaves is found in the sap of the vacuole.

Amino acids were differentiated with paper chromatography by Dr. van Die. In the sap the following amino acids were found: Asparagine, Glutamine and alanine, Glycine, Valine, Leucine–isoleucine Glutamic acid and Proline. In the press-sap from the leaves, about the same amino acids were found with the exception of Proline. The leaves also contained Threonine, Arginine and Serine. The total amount of amino acids in the sap of the leaves was about 470 mg/l. *Potassium* is evenly distributed, and about the same values are found in the leaves and in the vacuole sap. Of *Phosphor*, *Calcium* and *Magnesium*, quantities are smaller than those found in the leaves.

MICRONUTRIENTS

The following micronutrients were found. (Table II).

TABLE II

	Tree	Micronutrients in mg/l in sap or mg/kg in leaves					
		Co	Cu	Fe	Mn	Mo	Zn
sap	T 6	0.02	0	0	2	0.10	0.77
	T 8	0.02	0	0	0.5	0.02	0.76
fresh	T 6	—	0.95	24.7	11.5	12.5	3.4
leaf	T 8	—	1.05	21.8	6.2	8.8	3.6
dry	T 6	0.03	3.8	98.6	46	0.50	13.6
leaf	T 8	0.03	4.1	87.1	25	0.35	14.3

No *Copper* or *Iron* was found in the vacuole sap. *Cobalt*, *Manganese*, *Molybdenum* and *Zinc* were present in the sap.

DISCUSSION AND SUMMARY

Many of the nutrients found in the leaf-tissue of the coconut palm can be found in smaller quantities in the vacuole of the embryosac, with the exception of Potassium which seems to be more evenly distributed in both. This concerns P. Ca, Mg, Co, Mn, Mo and Zn. Copper and iron, though present in the leaf-tissue, were lacking in the vacuole sap.

Nitrogen in the vacuole was only found in ± 2 % of the amount present in the wet leaves. In the vacuole a considerable part of this nitrogen is present as amino acids. In general the same amino acids were found in the leaves and in the vacuole.

Comparison is also possible with sieve tube sap of palms (TAMMES, 1933, 1958). Differences between vacuole sap and sieve tube sap especially exist in:

1. vacuole sap ± 2 % monoses, sieve tube sap 15 % of sucrose.
2. Calcium ± 288 mg/l in vacuole sap, only 19 mg/l in sieve tube sap. Copper and Iron are found in very small quantities in sieve tube sap and are probably nearly absent in vacuole sap. As far as the other substances are concerned, the same elements, even the same amino acids were found in sieve tube and vacuole sap.

REFERENCES

PRÉVOT, M. et M. OLLAGNIER. 1954. Diagnostic Foliaire du Palmier à Huile et de l'Arachide. Plant Analysis and Fertilizer Problems, Paris.

SALGADO, M. L. M. 1954. The nutrient content of nut water in relation to available soil nutrient as a guide of manuring the coconutpalm. Plant analysis and Fertilizer problems. Paris.

TAMMES, P. M. L. 1933. Observation on the bleeding of Palm trees. Rec. Prov. Bot. Neerl. 30–514.

———. 1940. On the development of the coconut fruit and the factors which influence the copra content of the nut. Landbouw, Vol. XVI, pp. 385–395.

———. 1958. Micro- and Macronutrients in sieve-tube sap of Palms. Acta Botanica-Neerlandica, **7**: 233–234.

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THE BREAKDOWN OF CARBOHYDRATE BY SCHIZOPHYLLUM COMMUNE FR.

THE OPERATION OF THE TCA CYCLE

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(received June 10th, 1959)

The tricarboxylic acid cycle (TCA cycle), as proposed by Krebs and coworkers, has received widespread consideration in explaining the enzymatic reactions that bring about the breakdown of pyruvate to carbon dioxide and water. As a result of experiments with isolated mitochondria, the concept has arisen that the enzymes of the TCA cycle are localized mainly in mitochondria (cf. Schneider and Hogeboom, 1956). Although the scheme is apparently characteristic of metabolism in animal tissues, there is good evidence that it is at least potentially functional in higher plants, bacteria and yeasts. The operation of the cycle in molds however is still the subject of much investigation and controversy. Various workers have shown the presence of some or all of the individual enzymes of the TCA cycle (cf. Cochrane, 1958), but relatively little work has been done on the isolation of functionally active subcellular particles from fungi. (Bonner and Machlis, 1957). In this report some observations on subcellular particles from *Schizophyllum commune* are given.

METHODS

Organism

A non sporulating mutant strain of *Schizophyllum commune* Fr. (C.B.S. Baarn) was grown for 10 days at 27° on a medium consisting of 10 g glucose; 2 g asparagine; 0.5 g KH_2PO_4; 0.5 g $Na_2HPO_4 \cdot 2H_2O$; 1 g $MgSO_4 \cdot 7H_2O$; 1 ml trace-elements solution (Hoagland and Snijder) per 1000 ml water.

In order to promote growth 10 ml of a yeast-extract preparation was also added and pH adjusted to 7.0. Aeration was obtained by shaking in shallow culture. The submerged mycelium, which was exclusively dicaryontic, was harvested and washed with distilled water.

Disintegration and preparation of cell-free extracts

30 g prechilled mycelium (wet weight) was ground in a cold mortar with coarse acid-washed sand and a solution containing 0.8 M glucose; 0.05 M KH_2PO_4; 0.02 M nicotinamide (adjusted to pH7.0 with NaOH) during 10 min in the cold. The homogenate was filtered through cloth and centrifuged for 10 min at 800 g. The supernatant

fraction was centrifuged again for 20 min at 24000 g. The resulting supernatant was poured off, and the particulate fraction washed with 30 ml of the disintegration medium, spun down, and then resuspended in 7 ml of this medium. A Phywe refrigerated high-speed centrifuge was used.

Measurements of respiration

Oxygen uptake was measured in standard Warburg experiments at 30°. $QO_2 = \mu LO_2$ taken up/hr/mg dry weight, $QO_2(N) = \mu LO_2$ taken up/hr/mg protein. All values represent averages of duplicate experiments.

Estimation of protein

Protein was estimated spectrophotometrically by the method of Pardee. The protein of the particulate suspension was precipitated by adding one part 10 % trichloroacetic acid, centrifuged, and washed with distilled water. To the washed sediment the biuret-reagent was added and after incubation (45 min at 37°) the mixture was centrifuged, and the optical density measured at 530 mμ in a Beckman spectrophotometer.

Partition chromatography

The reaction mixture of each vessel was deproteinized by adding one drop of 0.5 N HCl and heating in boiling water during 2 min. The protein was spun down and 0.025 ml of the supernatant was spotted on Whatman No 1 paper. Ascending chromatography with n-butanol, acetic acid, water (4:1:5) as solvent during 24 h at 28° has been employed. Spray-reagent slightly alkaline bromophenol blue solution (Lugg and Overell, 1947). The R_f-values of the organic acid spots were compared with those of controls without incubation.

Substrates and coenzymes

Sodium pyruvate and the other TCA cycle intermediates, in the form of acids, were purchased from Fluka, Buchs, Switzerland. The acids were neutralized with an aequivalent amount of K_2CO_3, and shaken with air to remove CO_2. Also from Fluka: adenosine-5-triphosphoric acid or the tetrasodium salt (ATP), coenzyme A (CoA), nicotinamide, and hexokinase (28000 units/g at 30°). Diphosphopyridine nucleotide (DPN), "purest", C. F. Boehringer & Söhne, Mannheim Germany, and cytochrome c (cyt c) Fluka or Boehringer.

RESULTS

Intact mycelium metabolized glucose (0.05 M glucose in 0.05 M phosphate buffer pH 7.0) aerobically as well as anaerobically. The rates were QO_2: −33.4 and $Q^{N_2}_{CO_2}$: +32.5 respectively ($Q^{N_2}_{CO_2} = \mu L\ CO_2$ evolved in nitrogen atmosphere/hr/mg dry weight). Qualitative analyses of the incubation media showed formation of oxalic, citric and lactic acid under aerobic and citric and lactic acid under

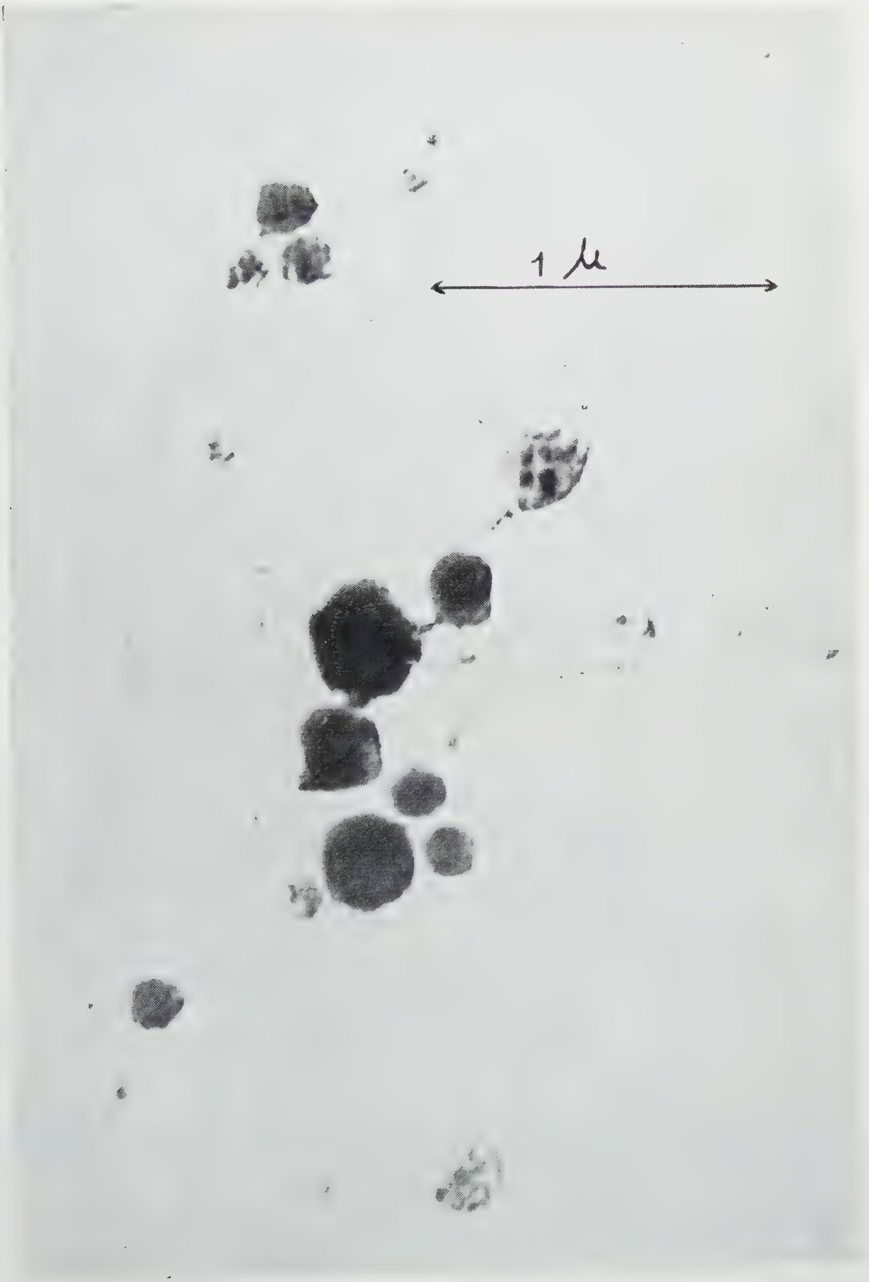

Fig. 1. Electron micrograph: normally prepared suspension of granules, fixed with a solution of OsO_4 in veronal-acetate buffer pH 7.2, (final concentration OsO_4 0.5 %) during 30 min, and washed twice with distilled water.

anaerobic conditions. The endogenic respiration was always very high (QO_2: —21.0). Cytological observations revealed great quantities of fat in the form of abundant droplets throughout all the cells, suggesting that this fat was the cause of the high endogenic respiration.

In order to abolish the impermeability of the cell-membrane for organic acids at pH 7.0, the mycelium was dried over P_2O_5 in the cold. The dried cells oxidized a variety of organic acids (0.025 M substrate in 0.05 M phosphate buffer pH 7.0). Stimulation of respiration rates in per cent of endogenic respiration, after 19 h drying, are shown in parentheses: pyruvate (25.8), citrate (17.7), α-ketoglutarate (21.6), succinate (30.5), malate (18.5). Prolonged drying of the mycelium diminished greatly the respiratory activity.

Cytological examination of the mycelium showed the presence of numerous granules in the cells, which stained readily with vital stains such as janusgreen B (Sorokin, 1938) and NADI-reagent (Perner, 1952). Rod-shaped particles, resembling the mitochondria of higher plants, could only be seen by using janusgreen B in a solution of 1 % glucose at pH 7.0 (0.05 M phosphate buffer). By staining in water the rods quickly fragmented and only spherical bodies could be observed. A complication with the NADI-reagent was the, probably secondary, distribution in the fat droplets of the indophenol blue formed. The isolated granules of the cell-free extract also showed a quick formation of indophenol blue with the NADI-reagent. Rod-shaped particles could also be observed after OsO_4-vapour fixation and application of the mitochondrial stain by Regaud (modification Bautz, 1955).

Electron microscopic observations on cell-free extracts, fixed in OsO_4-solution, revealed spherical granules with a diameter varying from 0.02 to 0.7 μ. The only particular structure observed in these particles was a system of smaller particles inside. (See Fig. 1).

An attempt was made to investigate the conditions for maximal respiratory activity of the cell-free extract. For succinate oxidation there was a stimulation of oxygen uptake by increasing the glucose concentration of the disintegration and incubation medium from 0.15 to 0.8 M. By further increasing the concentration the viscosity of the medium prevented the complete sedimentation of the small particles at 24000 g within 20 min. This also was the reason for the replacement of the sucrose, used in other studies, by glucose. Application of versene (0.001 M) in the disintegration medium did not appear to have advantages for the oxygen uptake, whereas addition of nicotinamide promoted the oxidation of oxaloacetate and pyruvate in the absence of externally added DPN, probably by inhibiting the breakdown of this compound. Hexokinase (300 units/vessel) addition had no effect on oxygen uptake. Below 0.025 M the substrate concentration (citrate and succinate) was limiting factor in the respiration rate. In all these experiments the not-varied conditions were according to standard experiments as given in Table I.

In such a typical experiment (Table I and Fig. 2) the cell-free extract showed oxidation of all TCA cycle intermediates (isocitrate

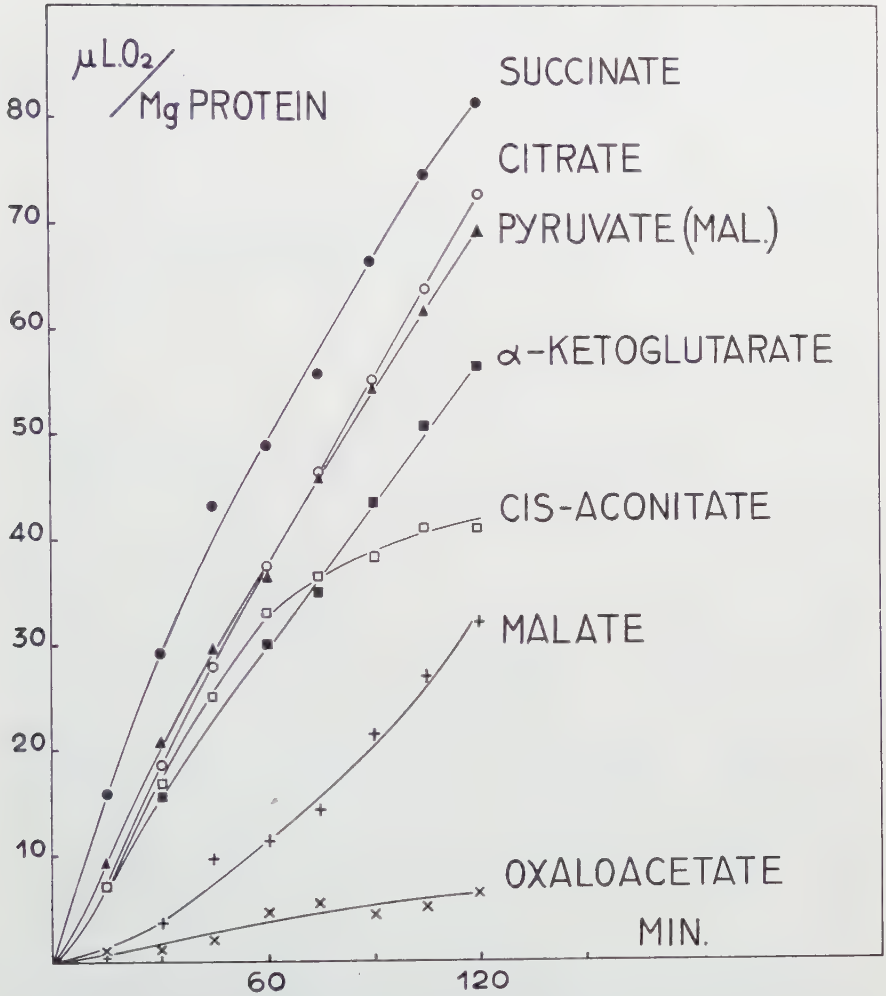

Fig. 2. Oxygen uptake with TCA cycle intermediates by the particulate fraction. Reaction mixture: see table I.

TABLE I

Oxygen uptake with TCA cycle intermediates by the particulate fraction. Reaction mixture: 0.8 M glucose; 0.05 M KH_2PO_4; 0.005 M $MgCL_2$; 0.01 M nicotinamide; 16×10^{-6} M cyt c; 0.003 M ATP; 3 mg DPN/vessel; 0.025 M substrate; 0.5 ml cell-free extract; final volume 3.0 ml; pH 7.0.

substrate	QO_2 (N)
pyruvate + 0.001 M malate	37.5
citrate	37.5
cis-aconitate	32.7
α-ketoglutarate	29.7
succinate	49.3
malate	11.3
oxaloacetate	4.0

and fumarate were also oxidized but no exact data are available). Although the enzyme system brought about the oxidation of pyruvate alone (QO_2 (N): —16.9), the addition of a small amount of malate caused a greatly increased rate of oxygen uptake (0.001 M malate alone QO_2 (N): —2.3), suggesting an oxidative condensation of a 2-c and 4-c compound.

Oxaloacetate was oxidized at a very slow rate. One assumption may be put forward: It is possible that externally added oxaloacetate, being a competitive inhibitor of succinic dehydrogenase (PARDEE and POTTER, 1948), inhibits its own oxidation via the reactions of the TCA cycle. This would be a situation analogous to the inhibition of succinic dehydrogenase by malonate, which inhibited not only the oxidation of succinate but also the oxidation of other TCA cycle intermediates (see Table III).

An interesting fact was the oxidation of malate. The oxygen consumption was low, and the curve showed a considerable lag phase, in contrast to the curves for the other acids. An explanation of these results may be put forward on the assumption that the rate of oxygen uptake was limited by the action of lactic dehydrogenase, with or without the "malic enzyme" of Ochoa (SALLES and OCHOA, 1950, KORKES *et al.*, 1950). In the case of lactic dehydrogenase activity this would imply formation of oxaloacetate, subsequent decarboxylation of this compound to pyruvate and a competition of lactic dehydrogenase and oxygen for DPNH. When the "malic enzyme" is also active, there can be a direct formation of lactate from malate via pyruvate, the "malic enzyme" competing with malic dehydrogenase for malate. In these cases one would expect the formation of lactic acid especially in the beginning, whereby the lag in the curve for oxygen uptake is explained.

Furthermore the requirement of the added cofactors was investigated (Table II).

TABLE II

Cofactor requirement of some oxidations by the particulate fraction. Control reaction mixture: as mentioned in table I. Rates of oxygen uptake were calculated on a basis of control = 100.

substrate	control	—DPN	—ATP	—cyt c	+ Co A (2 mg/vessel)
pyruvate + 0.001 M malate	100	45	116	—	208
citrate	100	37	124	—	—
cis-aconitate	100	46	90	—	—
α-ketoglutarate	100	83	33	—	203
succinate	100	160	49	43	—
malate	100	41	15	—	—

It must be noted that the data given in Table II cannot be compared mutually for the different acids, because they are the results of separate experiments. Omission of DPN greatly diminished the oxygen uptake with all substrates, except succinate. This fact can be explained by the DPN-linked formation of oxaloacetate, and the subsequent inhibition of succinic dehydrogenase by this compound. The omission of cyt.c caused a great decrease of oxygen uptake with succinate as a substrate. Addition of Co A resulted in a 100 % increase of oxygen consumption with pyruvate and α-ketoglutarate.

Some experiments were carried out to study the effect of malonate and arsenite on oxygen consumption with various substrates. Arsenite is known to block the sulphydryl groups such as in lipoic acid, a cofactor in the oxidation of pyruvate and α-ketoglutarate (PETERS *et al.*, 1946).

TABLE III

Influence of malonate and arsenite on oxygen uptake by the particulate fraction. Control reaction mixture: as mentioned in table I. To this medium malonate or arsenite was added in a final concentration of 0.001 M. No oxygen uptake with malonate (0.001 M) alone.

substrate	per cent inhibition	
	+ malonate	+ arsenite
pyruvate + 0.001 M malate	14.9	96.5
citrate	20.3	20.3
α-ketoglutarate	26.7	98.9
succinate	20.0	8.7
malate	5.5	46.0

The results suggest that oxidation of the various substrates is mediated by the reactions of a fully operating TCA cycle. An explanation remains to be found for the relatively low inhibition, by malonate, of the succinate oxidation as compared with citrate and α-ketoglutarate oxidation. It should be noted however that the oxidation of succinate is inhibited already for 20–40 % in the control medium (probably depending on the internal concentration of DPN) by the presence of externally added DPN.

The substrates and products of TCA cycle reactions were separated by filterpaper chromatography. The results are summarized in Table IV. Reaction mixtures after incubation under normal conditions were used (see Table I), inhibited by malonate and arsenite (see Table III), and reaction mixtures in which the glucose concentration was lowered to 0.05 M. In the last case oxygen uptake was diminished as compared with 0.8 M glucose mixtures as shown in parentheses: pyruvate + 0.001 M malate (30.9 %), citrate (37.3 %), α-ketoglutarate (46.9 %), succinate (36.6 %), malate (29.3 %).

It is evident that more reaction products could be isolated by lowering the osmolarity of the reaction mixture, possibly due to a loss of structural integration of the granules. After inhibition with arsenite no reaction products could be detected with pyruvate and α-ketoglutarate as substrates. Noteworthy is also the accumulation of citrate with all the substrates by inhibiting with malonate or by lowering the glucose concentration.

TABLE IV

Results of chromatographic analysis of organic acids formed by the particulate material. Reaction mixtures: as mentioned in table I (0.8 M glucose) respectively with lowered glucose concentration (0.05 M glucose), and addition of malonate or arsenite (see table III). Incubation time 120 min. The added substrate was always present yet on the chromatographs. At zero-time only a substrate spot could be detected.

substrate	0.8 M glucose	0.05 M glucose	0.8 M glucose + malonate	0.8 M glucose + arsenite
pyruvate 0.001 M malate	citrate	citrate	citrate	—
citrate	α-ketoglutarate malate ?	—	—	α-ketoglutarate
α-ketoglutarate	citrate	citrate	citrate	—
succinate	fumarate	citrate fumarate	citrate ? α-ketoglutarate	fumarate
malate	fumarate	citrate succinate fumarate	citrate fumarate	fumarate

DISCUSSION

The present work adds to the evidence for a certain similarity in the intracellular distribution of enzymes in higher fungi and other organisms studied. Dried mycelium and a cell-free extract, consisting of a particulate microscopically visible fraction, was shown to contain the enzymes necessary for the aerobic oxidation of the TCA cycle intermediates. The effect of cofactors and inhibitors, and the products isolated from the reaction mixtures strongly suggest that the TCA cycle is operating indeed in cell-free extracts of *Schizophyllum commune*. The physiological role of this cycle in the intact organism, however, is not yet fully established. The difficulty, how to relate the accumulation of organic acids in the environment by the intact organism under aerobic conditions to the presence of the enzyme system mentioned above, remains to be elucidated. Although the oxygen consumption observed with malate was low in comparison to that with other acids tested (except oxaloacetate), malate readily served as a sparker for pyruvate oxidation suggesting that malate was being oxidized to oxaloacetate. The experimental evidence suggests, however, that malate can be alternatively transfered to lactate. Preliminary observations on oxygen uptake indicated that this alternative mechanism is located mainly in the smaller particles. The results of BROWN and CANTINO (1955) are of interest here. They found that homogenates of *Blastocladiella* will dismutate malate to lactate without appreciable oxygen consumption. In this context it is important that under aerobic conditions *Schizophyllum* produced more lactic acid from glucose than anaerobically, a phenomenon which was pointed out for other fungi by Carson *et al.*, (1951), Brown and Cantino (1955) and Gentile (1954). A sequence in which reactions of the TCA cycle and an enzyme system such as the "malic enzyme" of Ochoa are involved will offer a plausible explanation for this aerobic formation of lactic acid.

This proposed mechanism for the formation of lactic acid, via the reactions of the TCA cycle needs, however, further investigation, and consideration must be given to the operation of a glyoxylic acid cycle (cf. Kornberg and Krebs, 1957) or another mechanism for the production "de novo" of 4-carbon compounds.

SUMMARY

Some observations have been made on a strain of *Schizophyllum commune Fr.*, concerning the activity of normal and dried mycelium and a cell-free extract containing a microscopically visible fraction. The results fit in with the assumption of a TCA cycle, operating in this fungus. The possible role of this cycle in the accumulations of lactic acid has been discussed.

ACKNOWLEDGEMENT

The author is greatly indebted to the late Professor T. H. van den Honert and to Professor H. Veldstra for their interest in his work and their valuable criticism.

REFERENCES

Bautz, E. 1955. Ber. D. Bot. Ges. **68**: 197.
Bonner, B. A. and L. Machlis. 1957. Plant Physiol. **32**: 291.
Brown, D. H. and E. C. Cantino. 1955. Am. J. Bot. **42**: 337.
Carson, S. F., J. W. Foster, W. E. Jefferson, E. F. Phares and D. S. Anthony. 1951. Arch. Biochem. Biophys. **33**: 448.
Cochrane, V. W. 1958. Physiology of Fungi. New York–London. 222.
Gentile, A. C. 1954. Plant Physiol. **29**: 257.
Korkes, S., A. del Campillo and S. Ochoa. 1950. J. Biol. Chem. **187**: 891.
Kornberg, H. L. and H. A. Krebs. 1957. Nature **179**: 988.
Lugg, J. W. H. and B. T. Overell. 1947. Nature **160**: 87.
Pardee, A. B. and R. van Potter. 1948. J. Biol. Chem. **176**: 1085.
Perner, E. S. 1952. Biol. Zentralbl. **71**: 43.
Peters, R. A., H. M. Sinclair and R. H. S. Thompson. 1946. Bioch. J. **40**: 516.
Salles, J. B. V. and S. Ochoa. 1950. J. Biol. Chem. **187**: 849.
Schneider, W. C. and G. Hogeboom. 1956. Ann. Rev. Bioch. **25**: 201.
Sorokin, H. 1938. Am. J. Bot. **25**: 28.

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A STUDY OF HETEROPHYLLY AND INFLORESCENCE STRUCTURE IN DENDROPHTHORA AND PHORADENDRON (LORANTHACEAE)

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(received June 23rd, 1959)

INTRODUCTION

It is not surprising that the mistletoes, being parasitic plants, should show a great range of diversity in the structure of their haustorial organs. These organs, after all, are involved in the act of parasitizing; they form the physiological channel for the materials which the parasite draws from its host. It can therefore be appreciated that such vitally important organs should have evolved in many directions, this evolution being influenced by different endophytic environments when new host species were attacked.

Much more puzzling, however, is the fact that many of the most striking morphological peculiarities in the mistletoe family appear not to be directly connected with the parasitic mode of life. The most outstanding of these are related to the flower and fruit, and a few of such features may be briefly referred to here: the absence of true ovules; behavior of the embryo sac (cf. MAHESHWARI, JOHRI and DIXIT, 1957); radical anther modifications in *Arceuthobium*, *Viscum*, and *Korthalsella;* the highly efficient explosive fruit of *Arceuthobium;* green endosperm, absence of rootcap, and presence of stomata on radicles of some Viscoideae (cf. KUIJT); and the peculiar inflorescence of *Dendrophthora* and *Phoradendron.* Before the full significance of such peculiarities can be appreciated, the structural variability of the organs involved needs to be explored in detail. I herewith present my observations on the morphology of the unusual inflorescences of the American genera *Dendrophthora* and *Phoradendron*, together forming the tribe Phoradendreae of the Viscoideae. I include some notes on the heterophylly so conspicuous and varied in many species of these genera, a phenomenon frequently important but sometimes used incautiously in the taxonomy of the Phoradendreae, and which is still poorly known in detail. It will be seen later that there are more relations between the seemingly separate topics of heterophylly and inflorescence morphology than meet the eye.

A few words must be said about the taxonomy of the two genera. The only distinction between *Dendrophthora* and *Phoradendron* which apparently holds true is the unilocular anther of the former as contrasted with the bilocular one of the latter. The question of merit of such a generic distinction I leave to the taxonomists to answer. TRELEASE monographed *Phoradendron* in 1916, but his treatment is open to much criticism, and is useful chiefly as a compendium of names and photographs of types. Even the species of North America can be determined in this monograph only with the greatest difficulty and uncertainty. The profusion of new species described and their vague delimitations have paralyzed critical work on the genus for many years. The only important taxonomic work since has been FOSBERG's (1941) revision of a number of North American species of *Phoradendron*. Note should also be taken of the nomenclatural change by JOHNSTON (1957) of *P. flavescens* to *P. serotinum* (Raf.) Johnston. Perhaps partly because of these taxonomic difficulties in this genus, and partly because of the difficulty in studying from herbarium material the morphology of the anthers (which are usually exceedingly small), the genus *Dendrophthora* has never been monographed. The division into subgenera by VAN TIEGHEM (1896*b*) is largely untenable (cf. URBAN, 1896) and is not directly relevant in this study. EICHLER's (1868) work is of lasting importance and will be referred to later. As to the taxonomy of especially the California species of *Phoradendron* I differ in some minor details from some of the above authors; but as a taxonomic discussion is not appropriate here I rely on accuracy of nomenclature to avoid possible ambiguities.

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I. HETEROPHYLLY

Plants possessing two distinct types of leaves are of fairly common occurrence. It is true, of course, that cotyledons and prophylls are usually of a different shape and organization than other foliar organs (quite apart from floral appendages), but such differences do not enter into the definition of heterophylly. The word heterophylly is, as it were, an expression of surprise that foliar appendages of distinct (though sometimes intergrading) types develop in positions on the plant body which seem to us quite comparable. It is in this vein that we may speak of heterophylly as it occurs in *Dendrophthora* and *Phoradendron*.

The various writers of the past have not, however, been consistent in their terminology. To avoid confusion, I shall first summarize previous usage of such terms as *prophyll*, *cataphyll*, and *scale-leaf*, especially as applied to the genera under consideration.

The term *prophyll* (from the German: Vorblatt) seems to have originated with C. F. SCHIMPER in 1834 (cf. RICKETT, 1954). Even in its first usage a comparison was made with cotyledons. In his morphological discussion of the Phoradendreae, EICHLER (1868) also speaks of the *prophylls* or *cotyledons* of the lateral branch. From later statements, however, we must conclude that Eichler regarded prophylls in these genera merely as the first pair of cataphylls. TRELEASE (1916)ignored the prophylls and their positions entirely.

JACKSON (1949) defines the *cataphylls* as "the early leaf-forms of a plant or shoot, as cotyledons, bud-scales, rhizomescales, etc.; in German, Niederblätter." Perhaps a more reliable idea of cataphylls can be obtained from GOEBEL (1923) who does not include cotyledons, and who gives numerous examples of appendages regarded by him as cataphylls. EICHLER'S (1868) circumscription of cataphylls in the Phoradendreae as a type of prophyll makes inclusion impossible of those scale-like leaves which occur on the percurrent axis of *P. paradoxum*, *P. crassifolium*, *P. piperoides*, and many others. In fact, it appears as if Eichler was confused as to the morphological nature of cataphylls in some of the species of *Phoradendron*, as he speaks of several pairs of scale-leaves *per internode*. Both Eichler and Trelease (at times) think of cataphylls as sterile organs. There are many examples, however, where cataphylls and prophylls subtend vegetative branches or inflorescences.

URBAN (1896) seems to have been a more acute observer of these details, and it is indeed regrettable that those following him have ignored his remarks on the Phoradendreae. He pointed out that every lateral axis, whether vegetative or reproductive, begins with two prophylls usually reduced to little teeth. He added, furthermore, some important facts concerning phyllotaxy of prophylls and the next higher appendages, to which I shall return later.

Before proceeding it is necessary to define the words in question. The definitions here used need not be accepted outside the Phoradendreae, but within the tribe some circumscription will, I think, be useful. The *prophylls* can cause little confusion if we adhere to the original meaning (cf. RICKETT, 1954) as the first pair of appendages, however small, and always of a transverse position, at the base of a lateral branch, whether vegetative or reproductive. When using TRELEASE'S (1916) work we should keep in mind the fact that he ignores the prophylls and associated characters; that when he speaks of basal cataphylls he refers to the second or higher pairs of appendages. *Cataphylls* as used in the present work shall refer to scale-like appendages of three possible positions. In some species cataphylls occur between pairs of foliage leaves on the main axis (*intercalary cataphylls*); in many, they are present between the prophylls and higher foliage leaves of the lateral vegetative axis. In the inflorescences of many species there are sterile scale-like leaves between the fertile ones and the prophylls (Figs. 6 and 7d); these may also be thought of as cataphylls. Sometimes a pair of cataphylls is fused to form a cup- or sheath-like structure, for which the expression *vagina cataphyllaris* (EICHLER, 1868) may be retained. Those scale-like appendages of inflorescences subtending flowers I shall call, not cataphylls, but fertile scale-leaves or bracts. All vegetative appendages (except prophylls and cotyledons) of the so-called leafless species are called scale-leaves. There are exceptional cases, however, in apparently leafless species where because of the tubular shape of a pair of fused appendages we must again resort to the expression *vagina cataphyllaris* (e.g. in *D. poeppigii*, Fig. 2a, and in *P. platycaulon*); and perhaps other difficulties will be discovered in due time. I am fully aware of the arbitrary character of such definitions and circumscriptions; but their usefulness as points of reference will, I hope, be better appreciated as the discussion proceeds. Finally, I wish to warn against the misuse of the term *internode* by Eichler (1868) and Trelease (1916). Both speak of the insertion of several pairs of cataphylls per *internode* or *foliage internode*. Such an extension of the concept internode is, I think, quite unwarranted and indeed confusing. The places of insertion of cataphylls, prophylls, scale-leaves and foliage leaves alike must be regarded as nodes; the areas between two successive nodes, as internodes, in accordance with ordinary morphological usage.

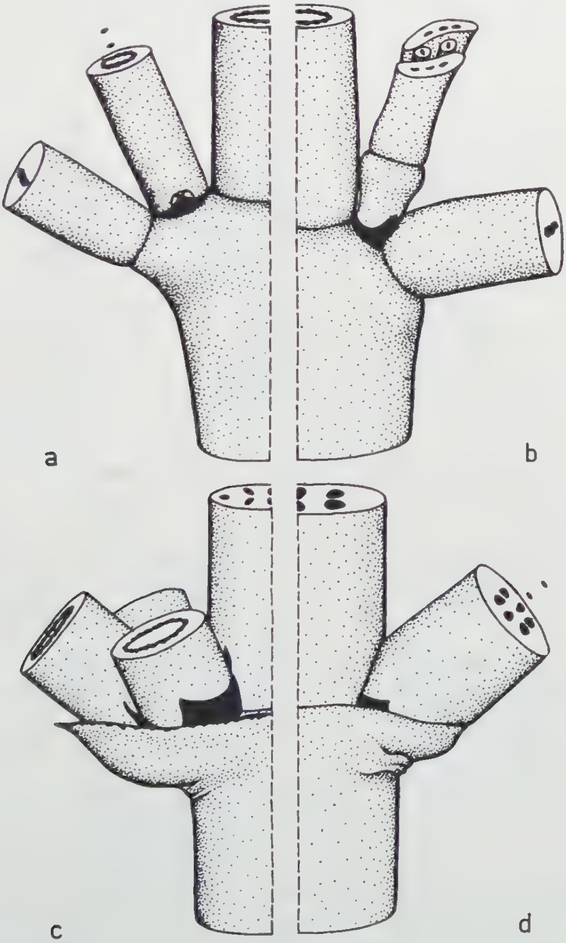

Fig. 1. Prophylls (in black) of a. *P. serotinum*, — b. *P. pauciflorum*, — c. *P. californicum*, — d. *P. juniperinum*. Dots above cut stem surfaces indicate the position of next higher appendages (× 7).

Prophylls The prophylls of the Phoradendreae are, as in many other Dicotyledons, minute structures. They are usually most clearly visible when young (Fig. 1b). Even then they may not be more than slight protuberances of the same color as, and not visibly delimited from the bulging shape of the node from which they arise. This is true, for example, in the species *P. villosum*, *P. macrophyllum*, and *P. serotinum* (Fig. 1a). In *P. densum* and *P. pauciflorum* the prophylls are somewhat more conspicuous (Fig. 1b). In the two latter species, which have expanded foliage, it is often easier to scrutinize herbarium material for prophylls because these organs are situated on the shoulder of the node, between the basal constriction of the subtending leaf and the also constricted base of the following internode of the main axis (Figs. 1a, b). In the "leafless" species, however, the pro-

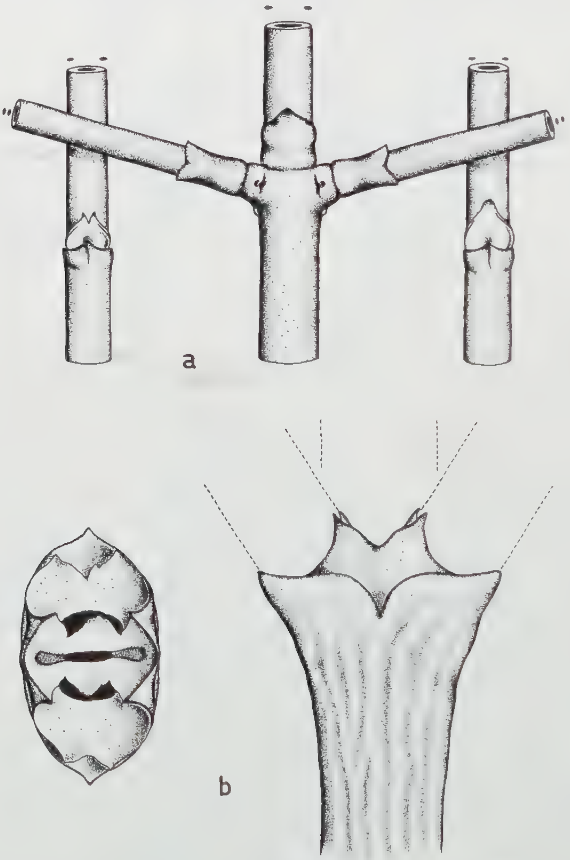

Fig. 2. a. Fusion of prophylls (left and right) in *D. remotiflora*, von Türckheim 2916, at U (× 3; lateral branches removed). Center: vaginae cataphyllares in *D. poeppigii*, Krukoff 6011, at U (× 3). Black spots indicate the positions of the next higher appendages. — b. Fused prophyll-pairs in *D. nipensis*, Morton & Acuna 3038, at K (× 6). Left, top view; right, lateral view. Main and lateral branches removed (broken lines).

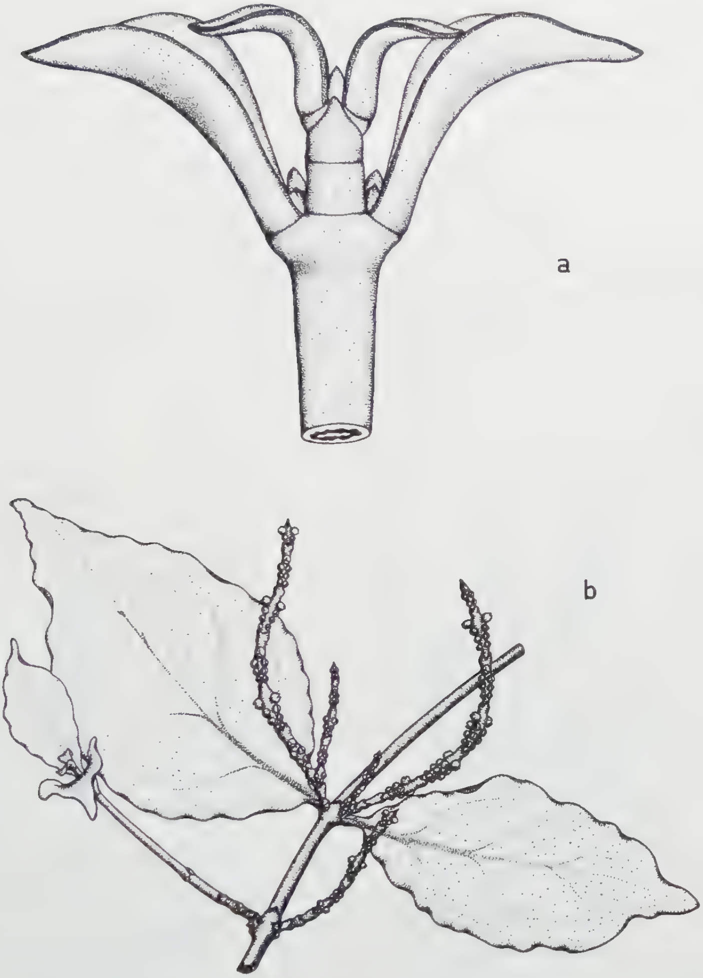

Fig. 3. a. Young foliage leaves and cataphylls of *P. piperoides* from Puerto Limón, Costa Rica (× 5). Kuijt 1529. — b. Mature branch of same (× ½).

phylls are usually at least partly obscured by the fused margins of the subtending scale-leaves (Figs. 1c and 1d). If branches develop in the axils of the prophylls of a primary lateral, such branches have their own pair of prophylls (Fig. 1c), or these may be wanting (see the secondary inflorescences of *P. pauciflorum*, Fig. 12b). In *D. biserrula* (Fig. 4a) the prophylls of secondary laterals are clearly visible as dark brown little teeth, even when these secondary branches do not themselves develop.

On older nodes it becomes progressively more difficult to discern the prophylls which may be obliterated or pushed aside by the expansion of the node. Indeed the position of prophylls on an herbarium specimen can, at times, be traced only from the inflorescences or other branches inserted in axillary positions. In *P. cheirocarpum*, for instance, lateral inflorescences of the fourth order may be present which do not appear to be subtended by any prophylls, yet emerge in the correct positions.

The fusion of prophylls in some species of *Dendrophthora* deserves a separate mention. URBAN (1896) mentions the fact that in *D. opuntioides*, *D. dahceri*, and *D. gracilis* the prophylls at times are fused and occupy a "monocotyledonous" position, i.e. above the lateral axis, opposed to the subtending leaf. According to my own observations, *D. domingensis* also has prophylls fused at least basally. In *D. remotiflora* this is true more consistently: the double prophyll is frequently notched, but may be apparently single (Fig. 2a). In the cases known to me the double organ is paper-thin and almost translucent, with a narrow upturned lateral edge. The process of fusion has gone one step further yet in *D. nipensis* (Fig. 2b) and some specimens of *D. domingensis*, where the four prophylls borne on one node form a single structure of, as it were, three toothed cups, the lateral ones containing the lateral axes, the middle cup the percurrent axis. Such a multiple structure gives the impression of being a very short internode.

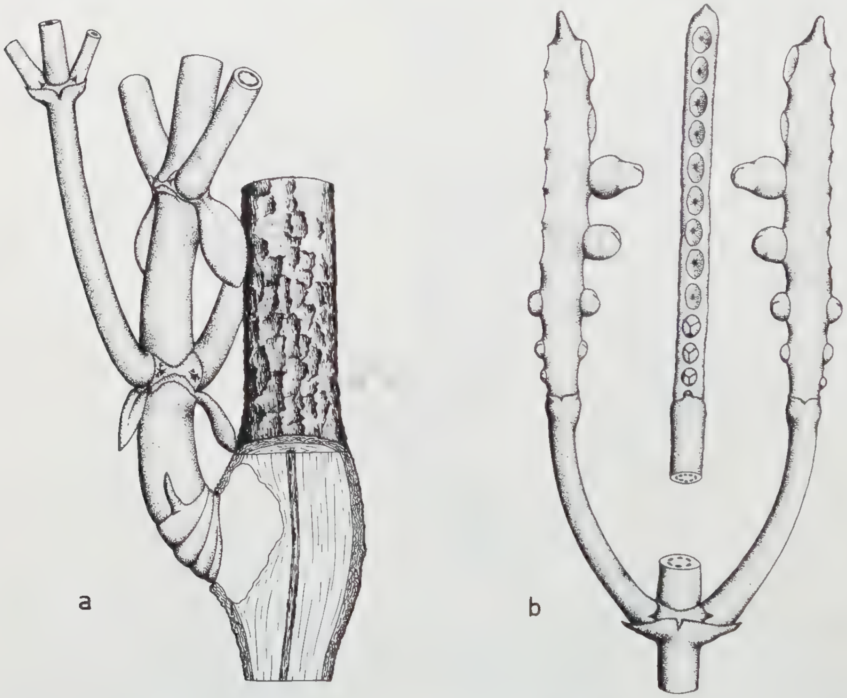

Fig. 4. *D. biserrula* (Kuijt 1532) on *Vaccinium consanguineum*, Volcán Irazú, Costa Rica. — a. Basal portion of young plant; haustorial organ left blank (× 1). — b. Lateral and median views of spikes (× 2).

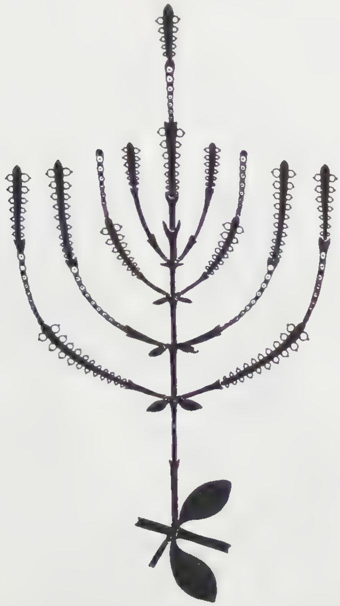

Fig. 5. Reconstruction of part of a plant of *D. paucifolia*, Williams 1530 (isotype, UC). Phyllotaxy must be thought of as decussate throughout (× ½).

Cataphylls Of the cataphylls I shall first deal with those occurring on lateral axes. They are frequently wanting on inflorescences. In all species north of Mexico (e.g. *P. macrophyllum*, Fig. 10a; *P. pauciflorum*, Fig. 12b), in *D. costaricensis* (Fig. 8d), *D. biserrula* (Fig. 4b), *D. ternata* (Fig. 9), and many others, the first pair of appendages above the prophylls is already fertile. In such species as *P. piperoides* (Fig. 6c), *P. crassifolium* (Fig. 14), *D. tetrastachya* (Fig. 7d), two to several pairs of cataphylls may intervene between prophylls and fertile bracts. Fusion of inflorescence cataphylls is the rule.

The cataphylls of vegetative laterals are, of course, more conspicuous because of the contrast with the foliage leaves above them. Those species of *Phoradendron* included by TRELEASE (1916) in his Boreales are without cataphylls. However, I would like to draw attention to the fact that in several species referred by Trelease to the "Brachystachyae" occasionally markedly reduced leaves occur near the base of a lateral branch. This phenomenon can be seen from Trelease's plates 51 (*P. globuliferum*) and 52 (*P. aureum*); I have also observed it in herbarium material of *P. brachystachyum* (Pringle 11160, L) and *P. minutifolium* (K.). We may perhaps regard such leaf reductions as an intermediate situation between presence and complete absence of cataphylls. The plants involved are also geographically intermediate.

In the "Aequatoriales" and in many species of *Dendrophthora* the cataphylls on lateral vegetative axes show a great variety of form, number, and prominence. Especially when only one or two pairs are found, these are often united into *vaginae cataphyllares* of shallow (*P. piperoides*) to tubular (*D. costaricensis*, *D. poeppigii*) shape. The second or third pairs, if present, become more shallow and more clearly bifid (*P. tonduzii*). In *D. poeppigii* the cataphylls form a conspicuous tube, almost completely obscuring the scar of the small deciduous leaf below (Fig. 2a).

I must now return to the matter of phyllotaxy of the first two pairs of appendages on lateral axes. URBAN (1896) is the only author who speaks of these features. He noticed that in *Dendrophthora* some variation

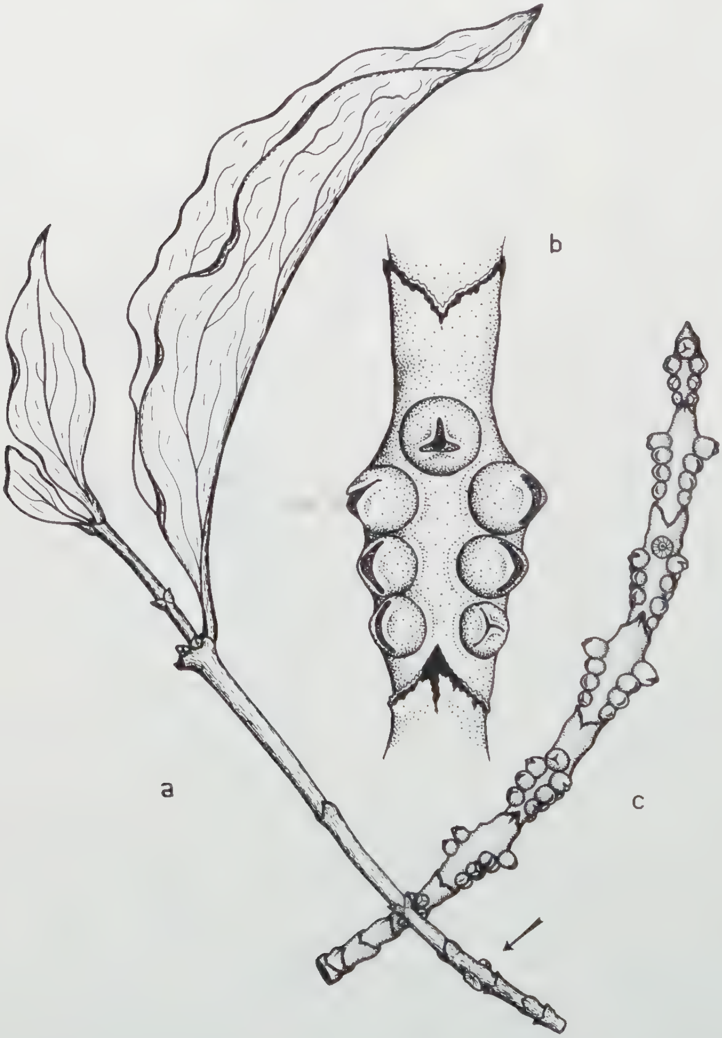

Fig. 6. *P. piperoides.* — a. vegetative lateral branch with pair of aborted flowers (arrow). Baber 2602, UC. — b. and c. Details of spike, Kuijt 1529 (× 1, × 8, and × 2 respectively).

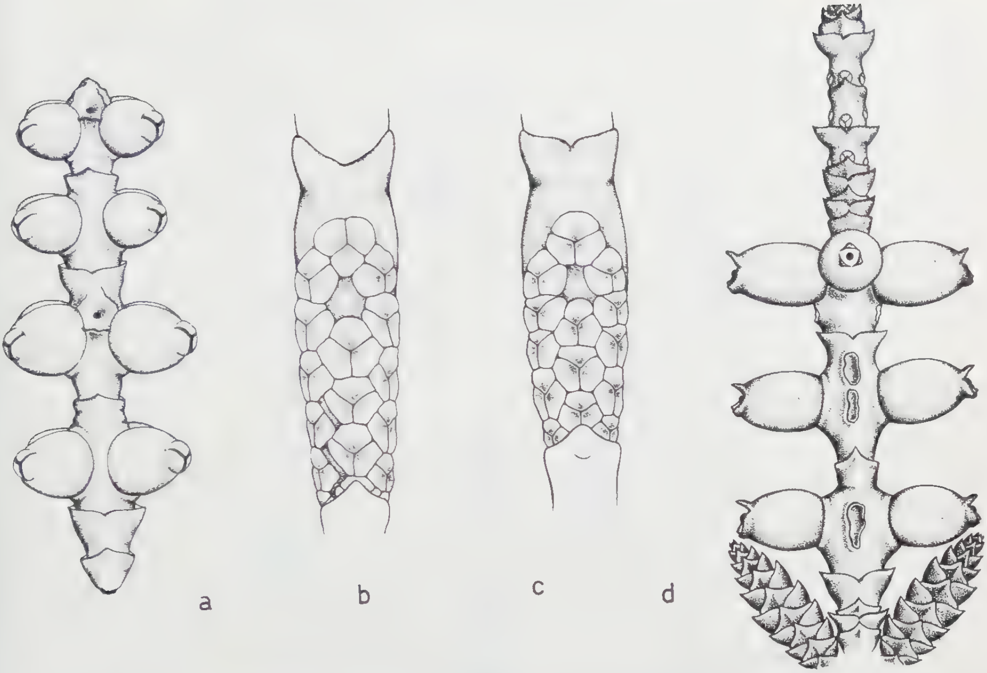

Fig. 7. a. *P. platycaulon* in fruit, the staminate (apical) flowers having fallen away (× 4). Spruce 228, the type, K. — b. & c. *P. tonduzii*, from Tres Rios, Costa Rica (× 6). Demonstrating the orientation of the apical flower b., when the second or more median flowers are absent; c., when the second or no median flower is absent. — d. Primary and young secondary spikes of *D. tetrastachya*, von Türckheim 3108, L (× 2).

exists in the relative positions of the prophylls and the next higher pair of appendages on the lateral axis. In one group of species, a decussate arrangement prevails throughout; i.e. the appendages following the prophylls are in the median plane. In the second group, however, the second pair of appendages stands transversely, in the same plane as the prophylls (distichous therefore), but beyond this second pair again a decussate phyllotaxy follows. Finally, there are those species which have a distichous arrangement throughout, sometimes with the exception of the basal portion of the plant.

Urban then moves on to look at these same features in *Phoradendron*, and concludes that all West Indian and South American species of this genus have one or more pairs of cataphylls or vaginae cataphyllares, the lowest being median in position, decussate thus with the prophylls. A decussate phyllotaxy is here thus the rule throughout the plant. Eichler (1868), indeed, had regarded this as a generic character. Urban had seen more material from North and Central America, however, and knew this to be incorrect. Again three different arrangements can be recognized, the first two remarkably parallel to the corresponding groups in *Dendrophthora*. Practically all South American

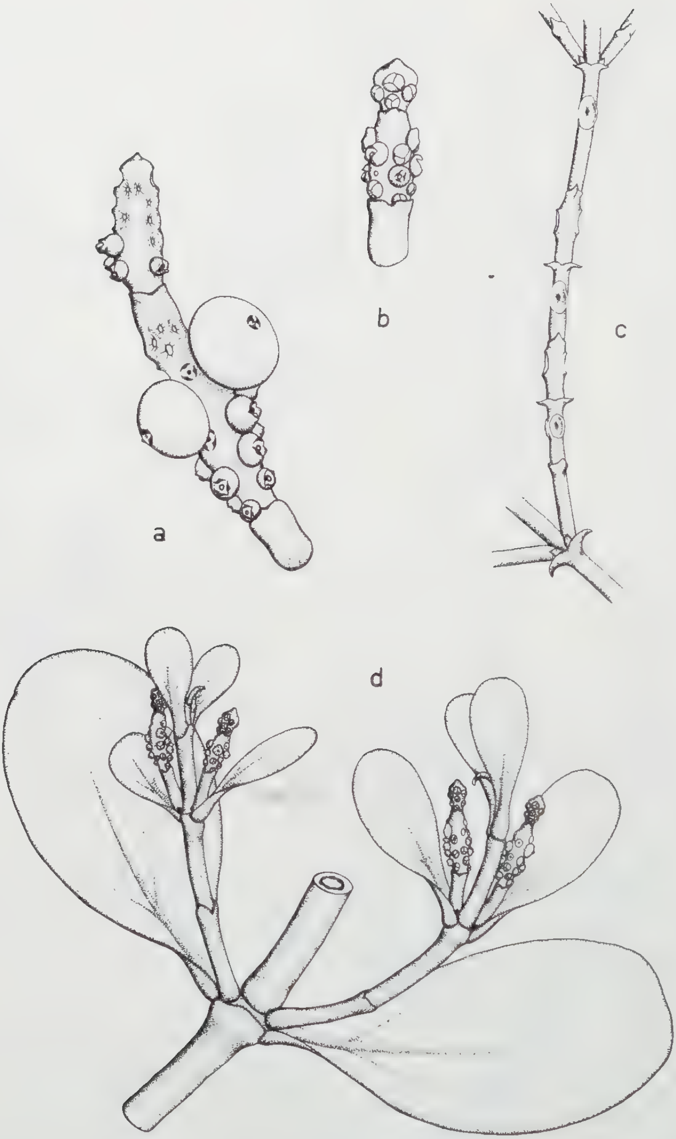

Fig. 8. a. & b. Inflorescences of *D. costaricensis* (Kuijt 1531) from Volcán Poás, Costa Rica; a. with mature berries ($\times 2^{2}/_{3}$).—c. *D. cupressoides*, branch with floral cups ($\times 3^{1}/_{3}$). Morris s.n., K.—d. Habit of *D. costaricensis* from the same collection as above. The two large lateral branches are secondary ones to primary inflorescences which have fallen away ($\times 1^{1}/_{3}$).

and West Indian species of *Phoradendron* have, as already stated, a decussate phyllotaxy throughout. To this group Urban adds *P. brachystachyum* and *P. tlacolulense* from Mexico. The second group has prophylls and the following pair of leaves in the same, transverse plane (distichous phyllotaxy), all others decussate. To this group Urban refers *P. serotinum*, *P. bolleanum*, and *P. minutifolium*. Finally, Urban groups together those *Phoradendra* which have scale-like leaves only, such as *P. juniperinum* and *P. californicum*. He also briefly refers to the remarkable fact that the prophylls and the next pair of appendages in *P. californicum* may be either decussate or distichous. I shall later return to this variation in phyllotaxy. I should mention here that Urban did not propose these divisions as natural taxonomic groups, but used them to underline these particular structural details.

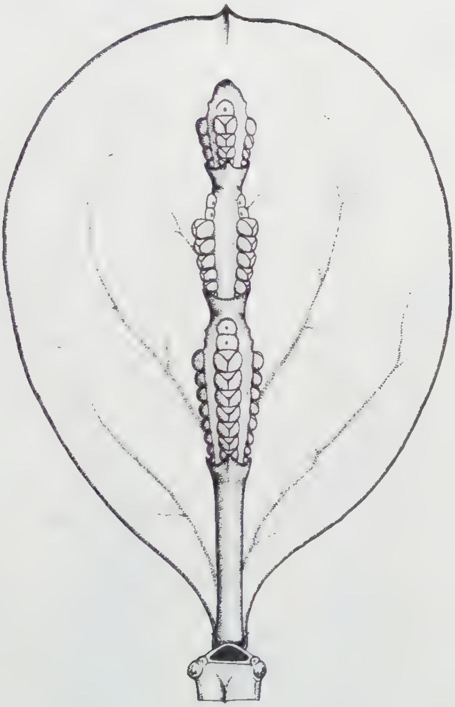

Fig. 9. Inflorescence (probably staminate) and leaf of *D. ternata*, Fuertes 1523 (the type), U. The two other leaves and two other spikes of the same node have been removed (× 2).

On the whole I find Urban's morphological categories helpful, but would make some changes. In *Phoradendron*, all of Trelease's Aequatoriales fit in group I (decussate phyllotaxy throughout). In group II, we may place all species occurring in the United States, except *P. californicum:* in *P. serotinum* (Fig. 1a), *P. macrophyllum* (Fig. 10a), *P. villosum*, *P. pauciflorum* (Figs. 12b, and 13a), *P. bolleanum* and *P. juniperinum* (Fig. 1d), the prophylls and the next higher pair of appendages stand in the same, transverse plane. Beyond, the phyllotaxy is uniformly decussate. It is difficult to know what to do with the

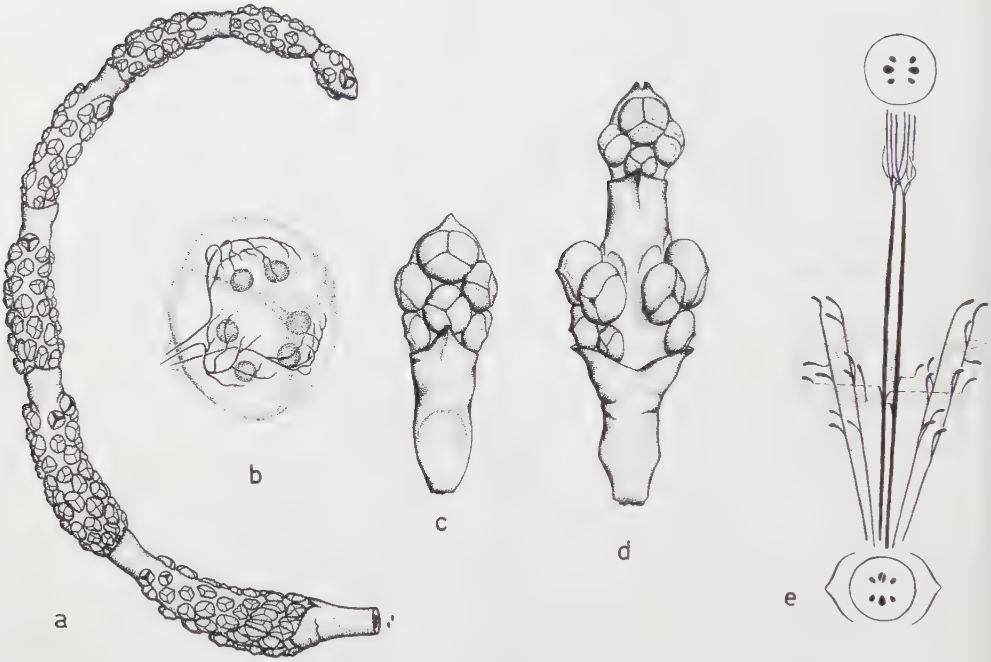

Fig. 10. a. Large staminate spike of *P. macrophyllum* from Woodlake, California (× $1^1/_2$); Kuijt 1209. Two dots indicate the positions of the subtending prophylls.— b. Staminate flower of *P. pauciflorum* (× 15), showing vascular structure. Kuijt 1521. — c & d. Staminate inflorescences of *P. pauciflorum* (× 6). — e. Diagrammatic representation of the vascular structure in the staminate spike of *P. pauciflorum* (× 10). Lateral traces somewhat pushed away from percurrent ones.

remaining species of the genus, as I have not seen sufficient material. I should prefer to retain them, tentatively, in a third group, because of the variation in phyllotaxy known from some of them. Urban hesitatingly speaks of this variation in *P. californicum* (see above). This species indeed shows an inconstancy in this respect. For example, Templeton 1559 (L) shows arrangements typical of group I and II on the same plant. Rehder 248 (K) from Arizona has decussate phyllotaxy throughout. Indeed, the decussate arrangement predominates in the various collections of this species which I have seen. In *P. brachystachyum* some plants are predominantly as group I (L 911–116–133), others as group II (L 911–116–136). In *P. calyculatum*, *P. velutinum*, *P. scaberrimum*, *P. tlacolulense*, *P. globuliferum*, *P. galeottii*, *P. diguetii* and *P. uspantanum*, all members of the Boreales, phyllotaxy again is decussate throughout, as in group I. It is an interesting fact that these are the most southerly representatives of the Boreales. In the matter of phyllotaxy therefore we find a continuous cline, from the Aequatoriales in the south and the adjacent Boreales (group I), through such species as *P. californicum* and *P. brachystachyum* (variable phyllotaxy), to the northerly Boreales where phyllotaxy is always as in group II. This morphological cline bridges the gap between the Boreales and Aequatoriales.

In *Dendrophthora* we find a variation in phyllotaxy which parallels that in *Phoradendron*. There are many species (perhaps most) which are decussate throughout, e.g. *D. biserrula* (Fig. 4a), *D. costaricensis* (Fig. 8d), and *D. poeppigii* (Fig. 2a). In *D. grisebachii* (Wright 2652, K), *D. glauca* (Wright 2651, K), and *D. cupressoides* (Morris s.n., K) the phyllotaxy again belongs in group II. In *D. tetrastachya* (Ekman 9540, K) both types of phyllotaxy occur on the same plant! *D. biseriata* (U 031249), though otherwise very close to *D. biserrula*, in contrast to this species belongs in group II. I have the impression, at

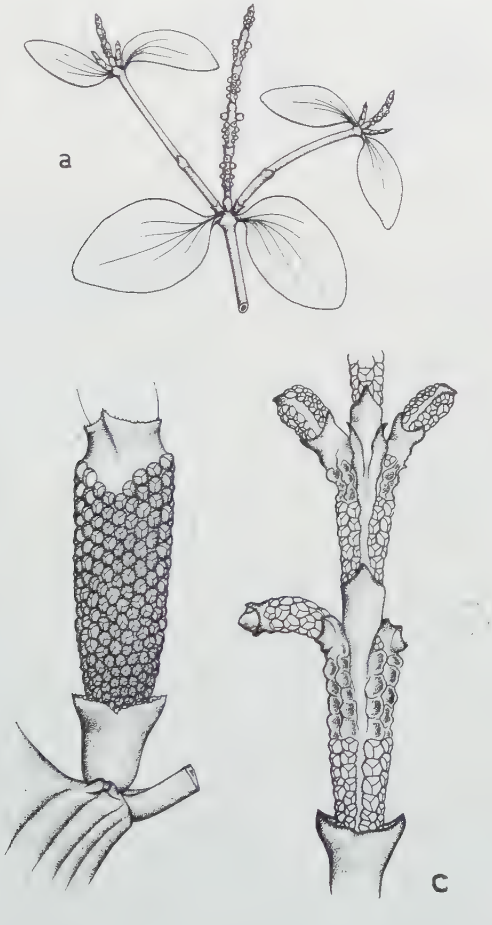

Fig. 11. a. Dichasial habit in *P. henslovii*, Habel 1868, K (× $^1/_2$). — b. Basal internodes of staminate spike of *P. calyculatum*, Pringle 13189, K (× 4). — c. Teratological staminate spike of *P. dimidiatum*, Boschwezen 5308, U (× 4).

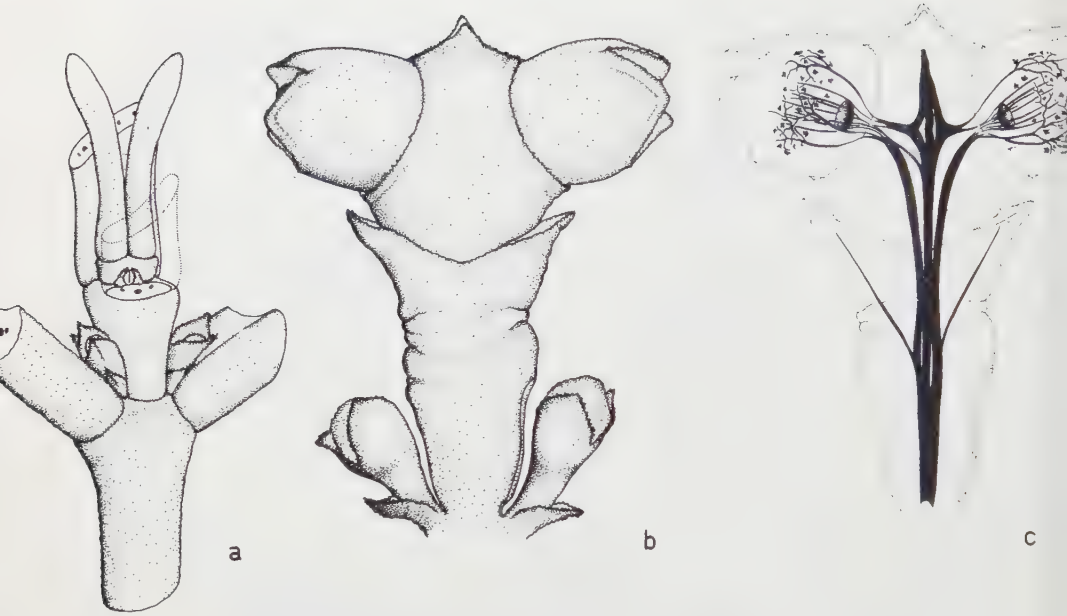

Fig. 12. *P. pauciflorum*, pistillate, Kuijt 1521. — a. Terminal part of branch with young inflorescences (× 5). — b. Primary inflorescence in fruit flanked by two young ones. (× 10). — c. Lateral view of the vascular structure of b (× 10)

least in *Dendrophthora*, that variation in phyllotaxy does not always correspond to the natural affinities of the species involved; that this variation in itself should not be overestimated as to its taxonomic significance. This point is also illustrated in the two European species of the related genus *Viscum*, *V. album* L. and *V. cruciatum* Sieb. ex Boiss. The former is decussate throughout; the basal leaves of the latter are in the same transverse plane as the prophylls (Tubeuf, 1923, p. 94). Yet there is no doubt that these species are very closely related.

There are, however, a number of species in both genera which also possess cataphylls on the main percurrent axis: these may be called *intercalary cataphylls*. For purposes of description it is useful to arrange them diagrammatically, as in Fig. 15, according to their increasing prominence of cataphylls. In *P. piperoides* (Figs. 3b and 15a), *D. poeppigii* (Fig. 2a), etc., cataphylls alternate regularly with foliage leaves. The cataphylls are inserted on very short internodes, the foliage leaves on very long ones, so that the former may easily be overlooked and the phyllotaxy appears distichous in *P. piperoides*. In *D. poeppigii* the intercalary cataphylls have fused to become vaginae (Fig. 2a); this is also true for *P. platycaulon* and *P. surinamense*. In *P. paradoxum*, two pairs of cataphylls are followed by two pairs of foliage leaves; then again two pairs of cataphylls, and so on. The lowest of a pair of these cataphylls is quite basal, the upper pair inserted at approximately equal distances to the foliage leaves above and below.

In *P. fendlerianum* two or three pairs of intercalary cataphylls follow upon each other, after which a pair of foliage leaves; then again a sequence of cataphylls, and so on. Approximately every third pair consists of foliage leaves, we might say, the others being cataphylls. Again the first pair of such a cataphyll series is basal, the others more evenly spaced between successive pairs of foliage leaves. The situation here differs from that in *P. paradoxum* only in that in the former one pair, in the latter two pairs of foliage leaves are inserted between two successive series of cataphylls. If it is true, as Trelease suggests, that that these names belong to different sexes of the same species, this would be an interesting case of sexual dimorphism. It is unfortunate that the two species have not been collected very often, so that the question cannot at present be clarified.

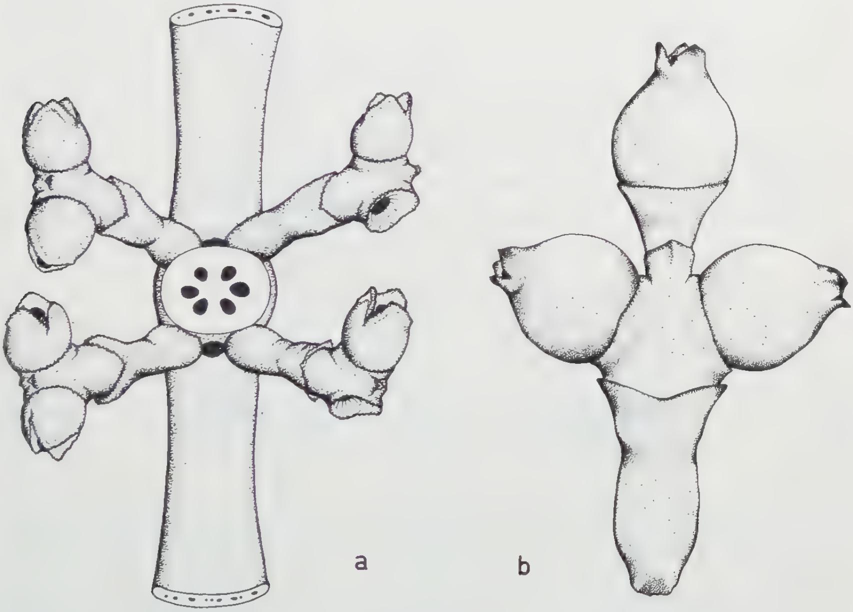

Fig. 13. *P. pauciflorum*, pistillate, Kuijt 1521. — a. Four secondary spikes in fruit the primary ones having fallen away (× 4). — b. Teratological spike with single terminal, pedicellate flower (× 7).

In the types of intercalary cataphylls mentioned sofar, only the foliage leaves subtend inflorescences. Cataphylls are not always sterile in other species, however. In *P. craspedophyllum* (Fig. 15d), for example, we find two pairs of cataphylls between every two successive pairs of foliage leaves, as in *P. fendlerianum*. The first pair of cataphylls is basal and sterile; the second, about midway between the foliage leaves, subtends inflorescences. The latter occur also in the axils of foliage leaves. The most advanced condition is seen in *P. crassifolium* (Fig. 14). Here the distance between two successive pairs of expanded leaves corresponds to one season's growth. Three or four

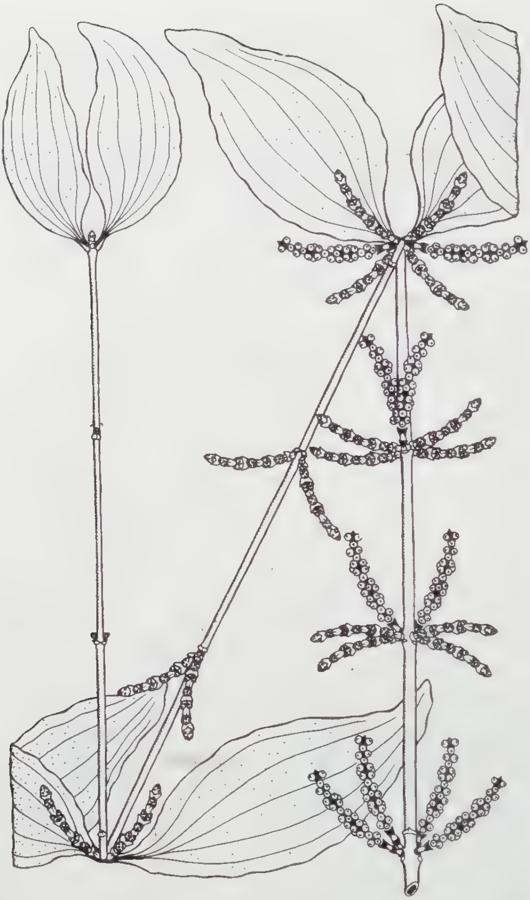

Fig. 14. Diagrammatic representation of the succession of inflorescences on a branch of *P. crassifolium* (× $^1/_2$). Based on Williams & Assis 6879, UC.

pairs of cataphylls are usually inserted along this length. The basal pair again crowns a very short internode, and is invariably sterile. The remaining cataphylls, as well as the foliage leaves, subtend inflorescences. In basipetal direction we therefore find portions of the main axis with successively more advanced inflorescences: first, a section with only inflorescence buds in the axils; then, fully developed inflorescences; finally, inflorescences in fruit and, in the axils of their prophylls, new inflorescences. The inflorescences axillary to foliage leaves always correspond in age to the inflorescences directly below. I shall later have occasion to return briefly to *P. crassifolium*, as it offers other points of interest.

From my own observations it seems that in those species of *Phoradendron* which possess intercalary cataphylls, the vegetative laterals bear at least as many as the sterile ones found in sequence on the main axis. In *P. piperoides* there are usually 1–5 pairs on lateral branches (Figs. 3b and 6a) occasionally up to 8 or 9 pairs (UC 142083). I have not as yet seen critical specimens of other types except *P. crassifolium* which has as few as one sterile pair of cataphylls on some vegetative laterals, as many as 4 or 5 on others. There are many species, of course, which have one (e.g. *P. liga*, *P. herbert-smithii*, *P. martianum*) or two (e.g. *P. quadrangulare*) pairs of cataphylls on lateral shoots, and none on the main axis.

It would indeed be very interesting to know at what age these types of heterophylly first appear. I suspect intercalary cataphylls to be absent from the juvenile aspect of plants which at maturity have them. This is only a suggestion, however, and only those botanists acquainted with the species in the field are in a position to supply such data. This also applies to that group of *Phoradendra* with a dichasial ("dichotomous") habit: from mature branches it is impossible to say whether such plants can develop intercalary cataphylls, because the axis terminates in an inflorescence. Only in young plants can be seen whether or not these cataphylls are a feature of the species.

Scale-leaves Reduction of leaf size is a very common feature in parasitic flowering plants. We see it conspicuously in *Cuscuta*, in *Cassytha*, in Balanophoraceae, Orobanchaceae, Lennoaceae, Rafflesiaceae. It is rather rare in Santalaceae (*Chorethrum*, *Daenikera*, *Phacellaris*) and among the parasitic members of Scrophulariaceae (*Lathraea*), and

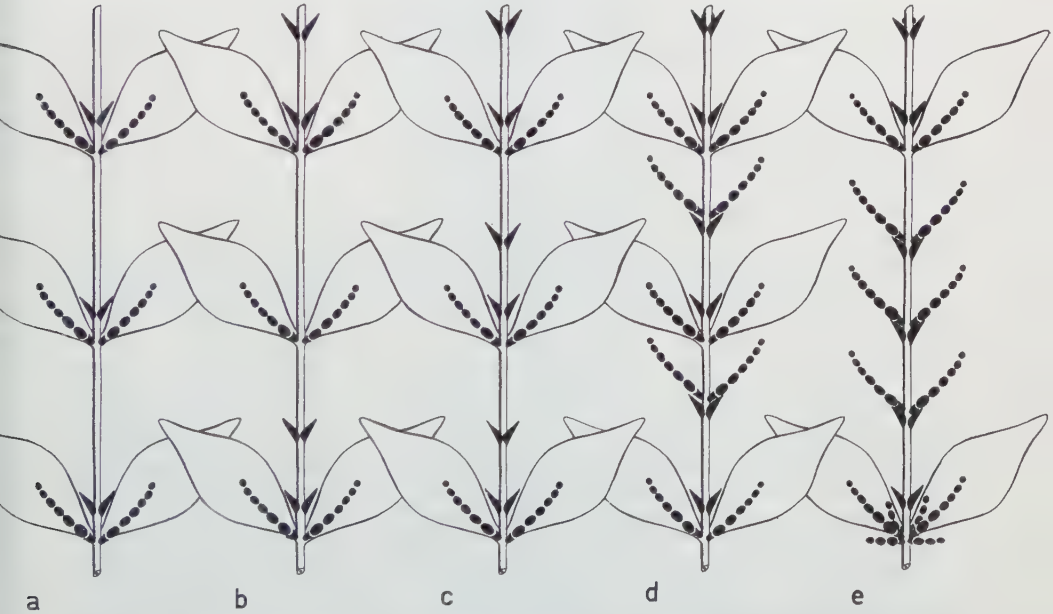

Fig. 15. Heterophylly and inflorescence position. Cataphylls and inflorescences are drawn in black. — a. Trelease's "Percurrentes" (cf. *P. piperoides*, Fig. 3b). b. *P. paradoxum*. — c. *P. fendlerianum*, *P. fanshawei*, and possibly *P. jenmanii*. — d. *P. craspedophyllum*. — e. *P. crassifolium* (cf. Fig. 14).

is known from Myzodendraceae in *Myzodendron* subgenus *Gymnophyton*. In Loranthaceae some genera are completely squamate (*Arceuthobium*, *Eubrachion*, and *Korthalsella*). Others have one or very few scale-leaved species (*Phrygilanthus aphyllus; Viscum minimum, V. articulatum, V. capense*). *Phoradendron* also has several squamate species, and *Dendrophthora* seems predominantly scale-leaved.

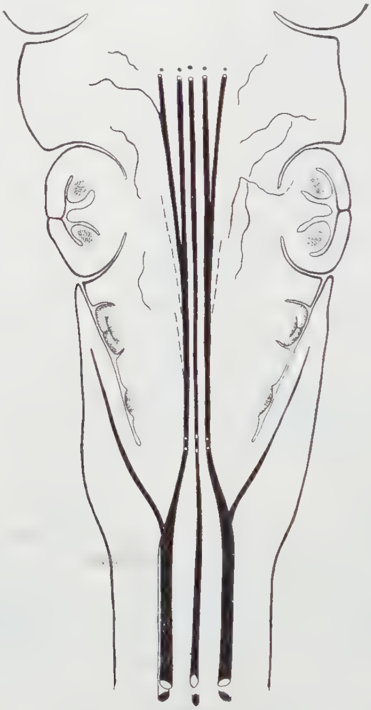

Fig. 16. Basal area of the spike of *D. biserrula*, Kuijt 1532 (× 8). Reconstruction of the vascular system and optical section. Only the nearest series of bundles is drawn fully; other bundles are indicated by cut ends only.

We cannot doubt, therefore, that many of the examples are of independent evolutionary origin. Consequently we should be exceedingly cautious in assessing the squamate character as an index to relationship, and should not hesitate to place together scaly and leafy species, or make a separation between squamate species, if other characters justify such decisions. Trelease's inclusion of *P. californicum*, for example, in his Aphyllae is in my opinion wholly artificial. The inflorescence, stamens, phyllotaxy and host range of this species show features quite different from comparable ones in the Aphyllae, and indeed in the Pauciflorae. Whatever the true position of *P. californicum* be, it can scarcely be where Trelease places it on the basis of its squamate habit.

There are, as far as I know, four species of *Phoradendron* with scale leaves: *P. californicum*, *P. juniperinum* (incl. *P. ligatum* and *P. libocedri*) *P. fragile*, and *P. tunaeforme*. Trelease places the first two in the Boreales; the last two in the Aequatoriales as they possess cataphylls on both lateral and percurrent axes. The fact that the cataphylls in these two species are fused and tubular like those of many leafy species seems to imply that the development of cataphylls and that of scale leaves are separate phenomena.

In the genus *Dendrophthora* there are a large number of squamate species. Of these may be mentioned *D. biserrula*, *D. domingensis*, *D. opuntioides*, *D. gracilis*, *D. cupressoides*, *D. squamigera*.

Perhaps the more interesting species, however, are those which have greatly reduced foliage leaves still larger than scale leaves. It is possible that in such species the same evolutionary processes are still at work which in others have already achieved the squamate habit. In some of these "intermediate" species we may discover a gradient

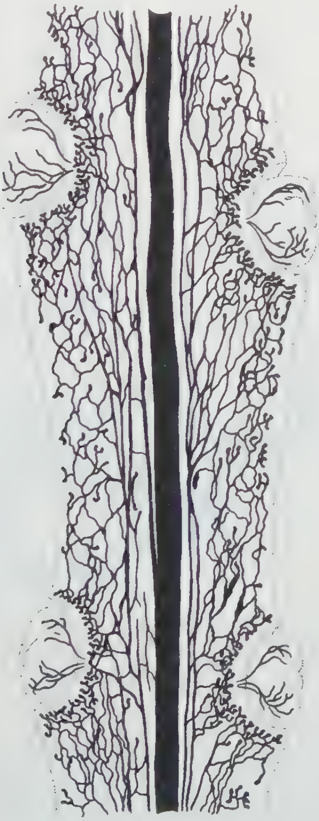

Fig. 17. Lateral view of cleared section of fertile internode of *D. flagelliformis*, Fuertes 374, U (× 8).

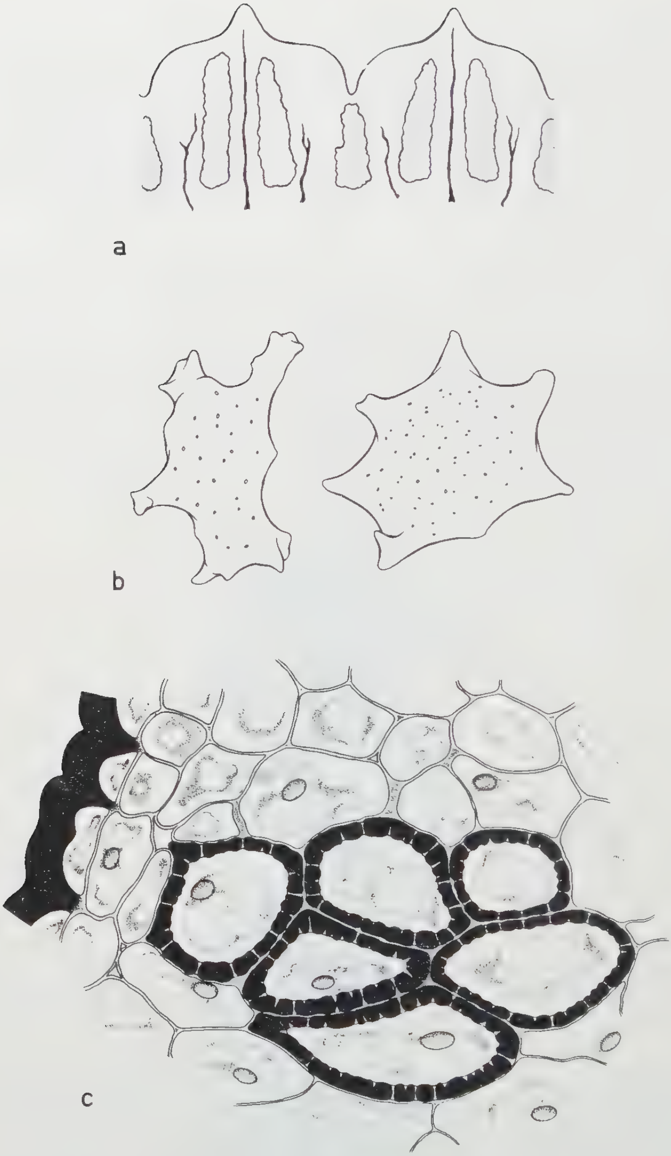

Fig. 18. a. Sclereid fields in the bracts of *P. piperoides* (× 15). — b. Sclereids from the spike of *D. biserrula*, Kuijt 1532 (× 150). — c. Cluster of sclereids in the spike of *D. biserrula*, Kuijt 1532 (× 150).

in leaf size. Following a lateral branch of *D. paucifolia* (Fig. 5) we find after the prophylls first a pair of cataphylls. The next pair of appendages, however, is suddenly the largest on that branch. From there on to the terminal inflorescence there is a steady decline in the size of leaves until the last ones are quite scale-like. The same pattern holds true for *D. biseriata*. Now it is interesting that a very closely related species, *D. biserrula*, seems to be in an even later stage of leaf reduction. It is commonly known as a completely squamate species. When one has the opportunity to inspect a young plant (Fig. 4a), however, the same gradient of leaf size is found for the base of a plant of this species, as that outlined for a branch of *D. paucifolia*. The lowest leaves are very small (cotyledons do not persist). Above these small scales, expanded though small foliage leaves suddenly appear, becoming smaller at the higher nodes until only scale leaves remain.

It again appears, therefore, that the development of cataphylls and reduction of foliage leaves to scale-leaves are two distinct evolutionary processes. The former seems to progress in an acropetal, the latter in a basipetal direction in the plants just mentioned. Indeed, the fact that many species have both cataphylls and foliage leaves shows the independence of the two processes. The circumscription of the concepts cataphyll and scale leaf on pp. 508–509 will now perhaps be better appreciated.

Entirely different patterns of heterophylly are, however, possible. In *D. grisebachii* we find series of 1–4 pairs of fully expanded foliage leaves near the base of the plant, and sometimes also higher up, immediately below the terminal inflorescence. These upper foliage leaves are separated by scale leaves from the foliage leaves at the base of the plant. No gradient occurs here. This is also true for *D. flagelliformis* where the base of the plant has large leaves which are suddenly, without transitional forms, replaced by scale leaves when we approach the inflorescences.

Any attempt to ascribe function to the cataphylls of the Phoradendreae appears doomed to failure by the very multiplicity these organs demonstrate in prominence, position, and frequency. It is easy to say that in *P. crassifolium* each series of cataphylls and that in *D. costaricensis* the basal cataphylls of lateral branches create a certain amount of space in which the inflorescences can better fulfill their function. At least some species of *Phoradendron* are entomophilous and a more prominent position of the spikes could amount to a real advantage. But what possible function could the majority of cataphylls have, supported as they are by internodes so short as to not provide any extra space whatsoever? Especially in such a case as *D. poeppigii*, a leafless species, the basal cataphylls could not be of any significance in this regard. The same seemingly inconsequential consistency and variation are to be seen in the petal positions of the flowers of these genera, a topic to be discussed in the next section.

II. Organography of the inflorescence

The inflorescence of the Phoradendreae is basically a succession of internodes with scale-like leaves arranged decussately. One or more terminal internodes are fertile; at least one, frequently several internodes above the prophylls are sterile. Flowers are arranged in "flower areas" each topped by a single apical flower above each scale-leaf of the fertile internodes, not truly axillary thus but rather distributed along the internode. The flowers are completely sessile in cup- or collar-like outgrowths on the axis of the inflorescence.

Eichler (1868) recognized three general types of inflorescences in *Phoradendron* which were delimited on the basis of the seriation of flowers. The first, the "2 × 2 type", had on one side of each fertile internode two series of flowers topped by a single, apical flower which stood exactly above the subtending bract. In the second, the "2 × 3 type", the apical flower was followed by a median, longitudinal series of flowers occupying the space between the two lateral series. In Eichler's third category we find elaborations of the second type into the "2 × 5, 2 × 7, and 2 × 9 types", which can be visualized by adding two, four and six additional lateral series to the three series of the previous ("2 × 3") type. These three categories are used by Eichler as aids to description, not as natural taxonomic groups. His remarks on the inflorescence of *Dendrophthora* are very incomplete.

Van Tieghem (1896*b*), on the contrary, made a taxonomic subdivision of each of the two genera on the basis of inflorescence morphology alone. In *Phoradendron* he recognized four sections. Section *Hexanthum* consists of species having only six flowers per fertile internode, one pistillate for each of the four lateral series, and one apical, median, staminate flower above each of the two bracts. Section *Tetrastichum* conforms to the remainder of the "2 × 2 type" of Eichler (to whom van Tieghem does not refer), with lateral series having more than one flower, except that the apical flowers are said to be staminate, the lateral ones pistillate. In section *Hexastichum* we find those species having three series of flowers above each bract, staminate and pistillate flowers being present in each series. Finally, section *Polystichum* contains those species having more than three series above each bract; this section can thus be equated to Eichler's third type.

A similar subdivision was proposed for *Dendrophthora*. Section *Diantha* unites all species having not more than two flowers, one above each bract, per internode. In section *Disira* this one flower per bract is followed by a single series of varying extent, each series containing staminate and pistillate flowers. The plants of section *Hexasira* develop three series of flowers per bract, each series having several flowers. In those cases where sexual dimorphism of inflorescences occurs, the staminate inflorescence, having the greater number of flowers, determines taxonomic position. In addition the new genus *Distichella* was segregated, differing from *Dendrophthora* in being distichous, and containing the species *D. opuntioides* and *D. gracilis*.

I shall not waste many words on Van Tieghem's taxonomic contentions; indeed Urban (1896) has already pointed out the unnaturalness of such groups. When so much morphological variation is subordinated to so few characters the resulting taxonomic system can only be artificial and unworkable.

Morphologically, Eichler's three categories are fairly useful. Eichler was, however, poorly acquainted with North American species;

furthermore, the inflorescences of *Dendrophthora* are not incorporated, or at most fit very awkwardly into his scheme. Van Tieghem's sections are, in my opinion, as bad morphologically as taxonomically. Furthermore, they are based on inaccurate observations and/or incomplete material. For example, the facts of sex distribution along a fertile internode which are implied for *P. latifolium* (= *P. piperoides*) in the section *Tetrastichum* are demonstrably incomplete or wrong; although they may possibly hold for other species. I have little choice, therefore, but group the inflorescences of *Dendrophthora* and *Phoradendron* in a manner which I consider more logical. Like Eichler, I do not wish such a scheme to be primarily a taxonomic one.

I wish to point out first a few features which are *not* taken into account in the classification below. The first of these are the number of fertile internodes per spike, and the number of flowers per series. These two features I know to vary greatly within some species, or differ between some closely related species and should, on the whole, perhaps not be taken too seriously. The distribution of staminate and pistillate flowers along an internode may be a constant character at the species level; but it would be difficult to incorporate such data in a general typology, not in the least because they are difficult to ascertain from herbarium material. In fact, the inflorescence types outlined below should not be adhered to rigidly, as different types are sometimes present on one inflorescence.

Type 1a. Apical flower followed by 2 lateral series; median series absent. By far the most common type in *Phoradendron* especially in the Aequatoriales; in the Boreales known only from *P. californicum*. In *Dendrophthora* it is found regularly only in *D. aequatoris* [1]). Sometimes found together with the next type, even on the same inflorescence (e.g. *P. tonduzii*). Where flower position is consistent, the apical flower is $^2/_1$, all flowers of the lateral series $^1/_2$ [2]). This is true for *P. demerarae* (Jenman 2546); uniformly in *P. racemosum*; in *P. anceps* (U 031029); in *P. tonduzii* when the median series is wanting; and in *D. aequatoris* (K). In others, however, though the apical flower always seems to be $^2/_1$, the lateral flowers may be quite irregular in position. This applies especially to the plants of *P. piperoides* which I have seen at Puerto Limón, Costa Rica. Here lateral flowers, though often $^1/_2$, are also frequently bipartite, and then usually $^1/_1$ (Figs. 6b and c). The regularity which Eichler (1868, see Tab. 31, ser. I, Fig. 1) implies for *P. piperoides* (*P. latifolium*) in any case is not evident in all plants of this species.

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[1]) I seriously doubt the appropriateness of Trelease's assignment (without any discussion) of this species to *Dendrophthora*. Indeed, Urban (1897) described it as *Phoradendron aequatoris*, and clearly spoke of a bilocular anther dehiscent by two pores.

[2]) I am following Eichler (1868) in the denotation of flower position. As a rule flowers are tripartite. When one perianth member of a flower is distal on the internode and the two others are inserted below, the flower position is said to be $^1/_2$ (e.g. the apical flower of Fig. 7c). When the opposite occurs we speak of a $\frac{2}{1}$ position (e.g. the apical flower of Fig. 7b).

It needs to be pointed out here that an inflorescence showing only three flowers (one median and two lateral) per bract cannot automatically be placed in this category. It is the position of the fourth and following flowers which is significant here. Where, as in the staminate spike of *P. juniperinum*, the fourth flower has a median position the inflorescence clearly belongs to the next, the 1b type. In *P. californicum* fertile internodes having four or more flowers per bract are exceedingly rare; and for this reason a rather outstanding feature of this species has remained undescribed. Where we do find a luxuriantly developed plant (e.g., Monnet 1128, Remy s.n., staminate, P; and Alexander, Kellogg and Carter 2002, pistillate, K), the fourth and later flowers of each bract are located in the *lateral* series. *P. californicum*, therefore, apparently alone in the Boreales, has a 1a inflorescence.

Type 1b. Above each bract flowers are inserted in three series, one median and two lateral. This type is found predominantly in the Boreales, e.g. in all species north of the Mexican border with the exception of *P. californicum*. It is also very common in the Aequatoriales. In addition, I have seen it in the following species of *Dendrophthora: D. costaricensis* (Figs. 8b and d), *D. buxifolia* (staminate), *D. chrysostachya, D. clavata, D. elliptica, D. epiviscum*, and *D. subtrinervis*.

Flower position in this type shows some interesting features some of which may here be recorded. In the staminate inflorescence of *P. pauciflorum* the apical flower is $^2/_1$, all others rather uniformly $^1/_2$ (Figs. 10c and d). The pistillate inflorescence of the same species bears only one flower per bract, and this flower strangely enough usually has the $^1/_2$ position (Fig. 2b). The (bisexual) spike of *D. costaricensis* (Fig. 8b) behaves like the staminate one of *P. pauciflorum*, though with occasional irregularities. In *P. tonduzii* (staminate), where usually three series are found per bract, all flowers are $^1/_2$ where the median series reaches up to the apical flower. It frequently happens, however, that the first one or more median flowers following the apical flower are absent, the median series being resumed below. In such cases the terminal flower commonly is $^2/_1$, all others $^1/_2$; in other identical situations all flowers are $^1/_2$ (Figs. 7b and 7c). The inversion of the apical flower is reasonably consistent, however, and was already noted by Eichler (1868).

In some species, especially in the larger Boreales (e.g. *P. macrophyllum*, Fig. 10a), the three series of each bract quickly loose their identity: the basic triplet pattern is not repeated regularly, flowers occur at irregular positions until no series can be recognized at all. The two flower areas of an internode may even coalesce below, flowers evidently being produced by a continuous intercalary meristematic ring at the base of the internode. The position of even the apical flowers of such spikes seems to be quite irregular.

Type 1c. This is really a modification of the previous type, 2, 4, or 6 additional lateral series per bract being added. I have seen very few of such inflorescences and Eichler mentions only *P. tomentosum* and *D. clavata* as having 5 series per bract.

In the *D. clavata* specimens at Kew (Hartweg 1044, Triana 2780, 4584, Holton 658, Tracey 119, 470, Balls 5730, Fendler 1114) I have seen only the 1b type, though with occasional irregularities. The type is not otherwise known from *Dendrophthora*. In *P. calyculatum* (staminate), 9 series are originally present above each bract (Fig. 11b). From the beginning both flower areas are coalesced and not separable. The series retain their identity for some distance downwards, but eventually become confused. Other species included in this type are *P. falcatum* and *P. robinsonii*. In the latter species (Pringle 9467, K) the lower flowers of an internode seem to be arranged in helices, a phenomenon also faintly discernable in *P. calyculatum* (Fig. 7b) and *P. macrophyllum* (Fig. 10a). Again, in these species there seems to be a continuous ring of florigenic meristem at the base of such internodes. Flower position in *P. calyculatum* is at first regularly $^1/_2$ but becomes irregular when seriation does. *P. tomentosum* and *D. clavata* (both 5 series per bract) are shown as being $^1/_2$ throughout in the Flora Brasiliensis, but I have not seen any material of *P. tomentosum*. In the *D. clavata* specimens cited above flower position was frequently irregular but otherwise $^1/_2$.

Type 2a. Flowers in a single median series only; therefore two series per internode. This is perhaps the most common type in *Dendrophthora* (e.g. Fig. 4b). It is not known from *Phoradendron*. Only in *P. jenmanii* (Ayliffe 14320, K) the inflorescence sometimes approaches this type. Often there are only 2 flowers of the basic triplet pattern in this species, the second flower apparently "taking advantage" of the absence of the third, and being developed towards a more median position, and sometimes directly below the apical flower. There is, however, so much variation in these features in *P. jenmanii* that the species cannot truly be accepted in this category.

Flower position in this type shows a remarkable consistency: only the $^1/_2$ position is found. I have seen no exceptions to this rule.

In very large staminate inflorescences of *D. domingensis* (Fuertes 1857, U) and *D. remotiflora* (v. Türckheim 2916, U) this median series sometimes proliferates laterally somewhat at the very base of the internode, so that a third or even a fourth series develops. Occasionally these additional series are in an intermedian position as in type 2c (see also below).

Type 2b. This type is really a unique modification of 2a, to my knowledge found only in *D. ternata*. Again, a single median series is present; but instead of being decussate the bracts (as well as the foliage leaves) occur in alternating whorls of three. There are therefore three series of flowers per internode. All flowers are $^1/_2$ (Fig. 9).

Type 2c. Flowers in four series per internode. One median series is found above each bract; in addition, there is one series above each sinus, or line of fusion, of the bracts. The latter series we may refer to as *intermedian series* (Fig. 7d). Strangely enough these intermedian series sometimes begin at a higher point on the internode than the median one, and also stop earlier. Flower position is $^1/_2$ throughout (Fig. 7d). I know this unusual type regularly only from two closely allied species of *Dendrophthora*, *D. sessilifolia* and *D. tetrastachya*.

There are species of *Phoradendron* which at first glance seem to belong in this category. In *P. platycaulon*, for instance, only three flowers develop per bract, one flower in each of three series. The apical flower is staminate and falls away very early. When the two other flowers (or four per internode) mature into berries, the scar and shallow cup of the apical flower is almost completely obliterated (Fig. 7a) and the inflorescence appears truly tetrastichous. On closer examination it can be seen, however, that these berries are in a lateral and not in a median or intermedian position.

It must be admitted that some of URBAN's (1896, pp. 284–285) remarks are disagreeable to the above typology. For a number of species Urban here describes irregularities which I have not seen, or at least not to the same degree. I have spoken of lateral proliferation in *D. domingensis* and *D. remotiflora* under type 2a. Urban reports the same for *D. biserrula* and *D. squamigera*, and even more conspicuously for *D. lindeniana*, *D. gracilis*, and *D. opuntioides*. Similar irregularities are cited for *D. buxifolia*, *D. chrysostachya*, *D. elliptica*, and others. I have seen lateral proliferations of this sort in *D. gracilis* (collector illegible, K) in *D. opuntioides* (Nicholl 55, K); but I have not seen the aberrant situations in *D. lindeniana* (Fendler 1113, K), or in any species with a 1b inflorescence. I wish to put on record a few collections of the latter type where, in contrast to Urban's observations, I have seen no irregularities: *D. buxifolia* (Wright 220, 221, p.p., K), *D. epiviscum* (Wright 221 p.p., K), *D. chrysostachya* (Lechler 1927, Balls 7265, K), *D. elliptica* (Gardner 437, 5727, Glaziou 3642, 6894, 8726, 17023, K). Among these aberrant forms Urban also lists *D. sessilifolia*, which I have placed under type 2b because of the regular intermedian series (Wright s.n., 1301, K). To what extent teratology here plays a role cannot as yet be decided. I suspect, however, that most of these irregularities are comparable to the ones discussed under type 1b.

Sex distribution on inflorescences

The identification of staminate or pistillate flowers from herbarium material is usually very difficult, if not impossible. Not only the small size of both flowers and anthers, but also the occurrence of prominent vestigial gynoecia make sex determination difficult unless fresh or preserved inflorescences are at hand. My statements on this topic are therefore partly based on indications in the literature which may not always prove entirely reliable; or the original author may have underestimated variability in this respect. Field observations can add much important information here.

There are many species, first of all, which exhibit a strictly dioecious distribution. This dioeciousness does not correspond with any known taxonomic boundaries. It is true that all of Trelease's Boreales are dioecious; but such species are also known from more southerly areas, in the Aequatoriales (according to Trelease, *P. wattii* is dioecious), and also in some species of *Dendrophthora* (e.g. *D. domingensis, D. opuntioides*).

Both staminate and pistillate spikes sometimes grow on the same plant. An example of this is *D. clavata*.

Bisexual spikes are present in both the Aequatoriales and in *Dendrophthora*. Within a single spike there may be a great constancy in the positions of staminate and pistillate flowers. In the *Phoradendron* cited by Trelease under *P. polygynum* (Fendler 1104) the lowest fertile internode bears staminate flowers only, all others pistillate ones. A similarity is seen in those inflorescences of *D. clavata*, which have one staminate and one pistillate internode, the latter being terminal. *D. clavata* appears to be unique in having such bisexual as well as completely unisexual spikes of each sex, even on the same plant (Hartweg 1044, K). KARSTEN (1859) claims that the apical flower above each bract of his *P. polygynum* is staminate, all others pistillate. In *P. platycaulon* (Fig. 7a) and others a similar pattern is present (see under inflorescence Type 2c.). *D. costaricensis* has not one, but three staminate flowers at the apex; strangely enough the oldest pistillate flower just below opens before the apical staminate flower on the same internode. In other species yet, such as *D. biserrula*, the lowest flowers are staminate, the upper ones pistillate.

Unisexual spikes can usually be easily distinguished from those of the opposite sex. The staminate spike always bears more flowers per internode, and sometimes more internodes per spike. These features can be seen in almost any of the North American species (*P. pauciflorum*, Figs. 10c and 10d; *P. macrophyllum*, Fig. 10a), but often also in *Dendrophthora*, for example *D. buxifolia, D. opuntioides, D. domingensis*, and *D. constricta*. As far as I am aware the staminate and pistillate spikes always are of the same type, though in the case of pistillate spikes with one flower per bract this can only be inferred.

Inflorescence and flower position

A few words may be said on the position of inflorescences on the plant. The most common situation is that which can be followed in Figs. 12a, 12b, and 13a for *P. pauciflorum*. Here inflorescences replace primary lateral branches, secondary spikes develop in the prophylls of primary ones, etc., in regular succession. Inflorescences of higher than the fourth order (*P. cheirocarpum*) are not known to me. Where intercalary cataphylls are present this regular sequence is interrupted, the lowest of the intercalary cataphylls being sterile in all cases. In a rather large number of species of *Phoradendron* (*P. henslovii*, for example) and in *D. poeppigii* shoots terminate in inflorescences, two lateral branches grow out at the base of such a spike, and a dichasial "compound inflorescence" is obtained (Fig. 11a). Thus a habit results differing from that of *Viscum album* only in the presence of two pairs of cataphylls on each lateral branch.

Indeed, there are many other instances where we may speak of compound inflorescences, where spikes are arranged in a constant pattern and together form a unit. *P. crassifolium* (Fig. 14) certainly is a case in point: the space between two successive pairs of foliage leaves forms a reproductive unit which is recreated annually. It is interesting to see that the spikes of this species are inserted somewhat above the cataphylls, and not truly axillary; perhaps this displacement is comparable to that of flowers by an intercalary meristem to the strange position they occupy in the spikes? Another type of compound inflorescence is very common in *Dendrophthora:* a shoot apex is replaced by a spike, and all laterals, instead of continuing vegetative growth as in the dichasial types mentioned above, also become spikes which arrange themselves symmetrically around the main axis (Fig. 5 for *D. paucifolia;* otherwise found in *D. cupulata*, *D. epiviscum*, *D. biserrula*, *D. flagelliformis*, and many others). In *D. biserrula* this symmetry is carried to such an extent that the two spikes developing from one node frequently are exact mirror-images (Fig. 4b), berries and flowers being present in precisely corresponding positions. Perhaps we can also think of *D. cupressoides* as having compound inflorescences: in this species the apical meristem of the spike simply retains its activity, and soon branches into ordinary vegetative growth (Fig. 8c). In the specimen of *D. tetrastachya* at Leiden (v. Türckheim 3108) several inflorescences have continued into a second inflorescence, built on top of the old one (Fig. 7d). In the Kew specimen of the same collection, however, nothing of the sort is in evidence, so that I do not know whether the Leiden specimen is teratological. To teratology must perhaps also be relegated what TRELEASE (1916) calls *P. piperoides* f. *composita*, with "a somewhat branched spike in some cases". I have not seen the specimen in question (Ule 4800) but I assume it to be of the same type as that of *P. dimidiatum* as illustrated in Fig. 11c. Here a small lateral spike occupies the place of each apical flower (even prophyll-like structures may be seen) of the main inflorescence. Interesting is also the inflorescence of *P. pauciflorum* drawn in Fig. 13b where the apical meristem of the spike has formed a pedicellate flower; and the *D. constricta* spike (Wright 220b, K) which, like the spikes of *D. cupressoides*, continues into a normal vegetative branch.

We may finally return briefly to the question of flower orientation, surely one of the most puzzling features of the Phoradendreae. Eichler, however hesitatingly, has speculated on the underlying causes of the consistencies and differences in the positions of floral segments. The ideas about torsion of flowers prevalent in those days are now, however, known to be without adequate factual basis or at least greatly oversimplified. The causal mechanism of phyllotaxy is nevertheless a matter of continuing controversy (WARDLAW, 1952), though experimental work is unearthing interesting new facts.

It must be remembered, however, that the flowers of the Phoradendreae originate under conditions quite different from those of subapically formed organs. Most importantly, these flowers are traceable, not to an *apical* meristem, but to an *intercalary* one. All except perhaps the apical flowers are formed just above the *mature* scale leaf. Which of the surrounding organs, whether bracts or older flowers, determines flower orientation remains a matter of conjecture. Even more puzzling is the variable position of the apical flower of *P. tonduzii;* for here it often appears as if the apical flower by its position ($^{1}/_{2}$ or $^{2}/_{1}$) determines the presence or absence, respectively, of the next few flowers of the median series. The apical flower in *P. juniperinum* and *P. pauciflorum* (which also have 1b inflorescences) is, on the contrary, of a $^{2}/_{1}$ position. When such discrepancy is found between two species having the same type of inflorescence we can scarcely make any generalizations as to the dynamics of flower position. Indeed, a more detailed study of the origin of flowers is needed before any hypothesis can be constructed. We shall have to know, for example, whether in a $^{1}/_{2}$ flower the apical perianth member is initiated before the others, or all three simultaneously. Until then we can do no more than draw a few general conclusions, though admitting the existence of exceptions:

1. a single median or intermedian series has flowers of a $^{1}/_{2}$ position.
2. in type 1a, the apical flower is most commonly $^{2}/_{1}$, those of the lateral series $^{1}/_{2}$.
3. if seriation is complete in 1b, all flowers are of the $^{1}/_{2}$ position.

These three points may be combined by saying that flower position in general is $^{1}/_{2}$, with the exception of the apical flowers of 1a inflorescences which are $^{2}/_{1}$.

4. there seems to be a necessary relation between regularity of seriation and regularity of flower position: if seriation deteriorates, the position of floral segments also becomes irregular.
5. the dominant positional effect perhaps emanates from the flower immediately above the one under consideration. This is indicated by the constancy of flower position in lateral series whether a median series is present or not; and by the apparent relation discussed under 4.

In the following part of this paper the vascular structure of the inflorescences of Phoradendreae will be discussed, and its evidence brought to bear upon the question of flower position.

III. Anatomy

The only previous anatomical work relevant to this study is contained in York (1913), who described the vascular structure of the inflorescences of *D. gracilis* and *D. opuntioides.* His observations will be introduced below; be it pointed out here, however, that the species studied by him have inflorescences with only a single median floral series (Type 2a). It cannot be surprising, therefore, that those inflorescences which differ greatly from York's species in external morphology are also different anatomically. Indeed, when considering the facts presented in previous pages it will at once be apparent that the remarks of the present section can be little more than exploratory.

I have attempted to study the vascular structure of several types of spikes, and with varying degrees of thoroughness. None of the descriptions below can claim finality or completeness; each represents a reconstruction or interpretation based on sectioned material, or cleared spikes, or both.

The vascular structure of the flowers appears to be rather uniform. The staminate flowers receive from the axial stele a single trace for each perianth segment. This vascular strand branches several times, the ramifications stopping well within the limits of the perianth segment (Fig. 10b). The sessile anther has no visible vascular supply whatsoever, a feature also found in other Viscoideae: *Arceuthobium* (JOHNSON, 1888), *Viscum album* (TUBEUF, 1923), and *Korthalsella* (MEKEL, 1935). The central cushion is also without vasculation.

The pistillate flower, in addition to such a vascular structure has a number of slender strands emerging from the very base of the flower and together forming a sort of spindle which is open towards the floral apex (Fig. 12c). SMITH and SMITH (1943) state that from ten to twelve traces are present in the pedicel of *P. villosum*, but I have not seen any material of this species. In *P. pauciflorum* the inner strands, which probably are of a carpellary origin, are held apart by a collenchymatous cup situated immediately below the ovarian papilla or mamelon. I have not been able to determine the exact origin of the "carpellary" traces, as they become exceedingly slender where the flower connects with the stem. The spindle formed by them delimits the space later occupied by the endosperm and embryo; indeed, these bundles form a conspicuous and beautiful silvery pattern against the dark green background of the endosperm when the seed is mature (this is also true in *Viscum album*: see TUBEUF, 1923, Fig. 64). Irregularly branched sclereids are present in a halo-like zone in the perianth of the pistillate flower only, but are absent from the remainder of the spikes of *P. pauciflorum*.

In other species of the Phoradendreae, however, sclereids are very abundant, and indeed can render observation of the vascular structure impossible in some cleared material, as in *D. biserrula*. In this species, as well as in *D. costaricensis*, a cortical zone about midway between the heavily cutinized epidermis and the stele contains a very great number of sclereids. They are somewhat branched and lobed, show an abundance of pits, and usually occur in small groups (Fig. 18b and c). They appear to retain a living cytoplasm and normal nucleus long after their secondary walls are heavily lignified in *D. biserrula*. In *P. piperoides* the clusters of sclereids are very large in the flower-bearing parts of the inflorescence. In the bracts of the same species sclereids occur in actual *solid fields* between the vascular traces of the bracts (Fig. 18a), each field uniting many scores of sclereids. Sclereids may also develop in the pith, as in *D. biserrula* and *D. costaricensis*.

The stomata, as typical in Loranthaceae, are transversely oriented on the stem. All superficial cells are covered with a thick cuticle. I can add no more details of the non-lignified tissues except that druses are frequent, especially in the outer cortical region of many species. I have seen fiber-caps on vascular bundles only in the peduncle of *D. biserrula*. The xylem elements vary greatly in length, and have secondary helical thickenings which tend to coalesce in the shorter elements. Evidence of stretched and obliterated elements is to be found especially in the oldest xylem of the base of a fertile internode. Most xylem elements appear to be vessel members with single terminal perforations. In the xylem of *P. californicum* there are short bulging vessel members each of which contains a large druse, a cell-type which is not known to me from any other plant. The vascular bundles are of the collateral type, but sometimes a group of small cells in the position of internal phloem reminds one of the bicollateral bundles known from *Viscum album* (TUBEUF, 1923).

It is now necessary to recapitulate YORK's (1913) work on the vascular anatomy and floral ontogeny in the spikes of *D. opuntioides* and *D. gracilis*. According to him, 6–14 bundles enter the spike from the main axis, these bundles being arranged in a dictyostelic way. There is no interfascicular cambium. The first fertile bracts receive one trace each, leaving the majority of the bundles to enter the lowest fertile internode. Here, as two parallel rows, they run essentially unchanged into the second fertile internode. In the meantime, however, several branches have been given off. From near the base of the internode, the two bundles closest to each bract (thus together four bundles) give rise to traces which ramify somewhat and are said to terminate in the swollen collar which surrounds the flower. These same four bundles supply three traces for each of the two flowers (YORK's Figs. 7 and 8). I have not myself been able to use material of York's species. Nevertheless, I cannot accept his description without question; it makes an altogether too simple impression. Be that as it may, York's description corresponds only partly with my own observations on other species.

The earliest sign of flower development, according to York, is a bulging out of the periblem of the axis some distance above the axil of the fertile bract. The collar now expands rapidly, almost burying the young flower in the axis. "Two cycles of floral segments develop acropetally on the young axis of the flower. The outer consists of three parts, which are the segments of the perianth; while the inner is composed of two segments, the carpels. The perianth completely covers the apex of the floral axis before the carpels have begun to develop. The two carpels arise as distinct primordia, and upon elongating inclose the moundlike apex of the floral axis between them. At this period of development the flower is still sunken in the axis of the spike, and its various parts are clearly distinct from one another. The apical growth of the floral axis is never active, and the outer region, composed of torus and the basal portion of the carpels, now grows rapidly, and thus the axis with the narrow ovarian cavity about it becomes deeply sunken within the torus." (YORK, 1913, p. 97).

Again, I cannot add to or criticize this description. In my own work I have seen young flowers of several stages, but none of these show the acropetal development, or the longitudinal extension of floral elements while covering the floral apex. Nor have I seen the near-burial of young flowers. Instead, in *D. biserrula*, the embryonic flowers appear more active than the collar. In even the youngest flower with distinct floral elements, the latter were closely appressed and in fact scarcely separable. Is it possible that we are here faced with a unique floral ontogeny through schizogeny (cleavage)? This seems a fantastic suggestion, but we must keep in mind that Loranthaceae are structurally aberrant in many ways. My own work does not allow critical observations, but the question is obviously one of great interest.

It is in any case true that the vascular bundles of the young flower have to be fitted onto a stelar organization which already exists. Even by the time the archesporium becomes recognizable in the staminate flowers of *D. biserrula* (when the flower begins to emerge above the bract) the flower is still without mature xylem elements.

It is perhaps most logical to consider first two species which have the same (2a) inflorescence which York's species had. Both of these species have a fairly large number of flowers per bract. The first, *D. biserrula*, has only a single fertile internode; the second, *D. flagelliformis*, up to a dozen fertile internodes per inflorescence.

The peduncle, or sterile internode, of the spike of *D. biserrula* contains six, but sometimes five or seven vascular strands arranged in a cylinder (Fig. 16). A single trace leads into each bract. Partly because of the varying number of bundles in the peduncle, and partly because of the density of sclereids there, I have not been able to ascertain the exact origin of the bracteal strands. It is certain, however, that they do connect with the stele at that point, and do not run down alongside it independently as York stated for *D. opuntioides* and *D. gracilis*. The percurrent bundles become extremely slender when entering the fertile internode. By this time they have aligned themselves into two series which are approximately parallel, an arrangement which persists and becomes more obvious in older parts. The traces leading into the flowers spring from the outermost bundles of each series. In addition a few small strands radiate out into the areas between the flowers. They do not branch and are difficult to follow because of their irregular course and slenderness. It is possible that these strands correspond to York's "collar traces". Since they are not, in *D. biserrula*, specifically directed towards the collars, this terminology is here inappropriate. Except for the percurrent bundles, no vasculation occurs below the rim of the bracts. Procambial strands diverging from the stele and extending towards the flowers can, however, be distinguished in this region (broken lines).

In the spike of *D. flagelliformis* a rather startlingly different organization prevails. The fertile internodes of this species are frequently flattened in the median plane of the subtending bracts. A portion of a cleared fertile internode is illustrated in Fig. 17. The skeletal system must be thought of as a double series of vascular bundles, one series partly obscured by the nearest. In the central part of the stem two strong percurrent bundles are present. These have only occasional and irregular connections with the remaining vascular system, and run into the next higher internode. On either side of this central pair of bundles there is a complex and highly irregular reticulum of slender bundles which ramify and anastomose. Some terminate within the spaces of the reticulum, others near the margins of the flattened stem, but always such vein endings are slightly thickened. A conspicuous aggregation of these vein endings may be seen in the floral cup, not only at the floral pedicel, but also in all other areas of the cup, even in its very margin. Because of the extreme slenderness of floral traces I have been unable to establish their precise origin, but I assume the connections are with some of the aggregating bundles of the reticulum. Although the majority of the veinlets below the flower point in its general direction we can obviously not speak of a vascular supply exclusively associated with the flower. The most central part of the reticulum shows a more consistently longitudinal direction. The reticulum is continued well into the following bracts. This, in turn, makes it difficult to discern the course of the bundles in the transition zone of the next internode. Each of the percurrent bundles forks while giving rise to a single median tract for the bract above it. In addition to the resulting four percurrent bundles a few very slender ones of the reticulum pass into the next internode. A fusion of some of the lateral bundles must somehow take place in the transition zone, as a pair of central percurrent bundles again is present in the next internode, and this pair is arranged in a plane at right angles to the corresponding plane of the previous internode.

We find in this species, therefore, a remarkably deviating axial structure which seems to be an elaboration of the more simple situation as seen in *D. biserrula*. It might be mentioned in passing that the stelar concept has little significance in such structures (cf. also *P. californicum*), as a stele can scarcely be delimited. We can only conjecture as to the functional meaning of the reticular aggregation of bundles near the flower. Could the floral cup here in its early stages somehow function as a placenta for the flower?

The fact that these two species are congeneric with *D. costaricensis* would lead one to suppose that this species, although instead of a 2a inflorescence it has a 1b type, might also show a reticular skeleton of some sort. This supposition turns out to be quite incorrect. The vascular structure of the spike of *D. costaricensis* does not appear to be appreciably different from that of the staminate spike of *P. pauciflorum*, which is to be discussed below. A feature which is more fully developed in the former species, however, is the vasculation of the first bracts. Three traces, often branching, supply these organs in *D. costaricensis;* in *P. pauciflorum* this number is usually, but not always, reduced to one median trace only.

Six bundles enter the first fertile internode of the staminate spike in *P. pauciflorum* (Fig. 10e), these being arranged in two parallel series of three each. The central percurrent bundle of each series is the largest. The large median gaps above the axils of the bracts are formed by the departing median bracteal traces below. If any lateral traces are present in the bracts they emerge from the other four gaps.

In a general way the origin of the vascular supply of the flowers corresponds to the origin of the bracteal bundles. The bundles leading from the median flowers connect to the two bundles delimiting each median gap. The traces leading from lateral flowers combine with these same bundles or with the percurrent bundles, according to the position of the floral segment involved.

The representation in Fig. 10e is, of course, highly diagrammatic, and is in reality rarely materialized. It is fairly common that, instead of six, five or seven bundles enter the fertile internode. The two bundles above each bract frequently fuse at points between two successive median flowers. In such areas a transection of the spike reveals four main bundles, each of the four gaps issuing traces to the lateral flowers in a cruciform overall pattern. Finally, the four terminating bundles occasionally show a very slight, upturned connection with the percurrent ones. It is of some interest that not all traces depart from longitudinal bundles in the usual upward direction: some turn downward slightly, and appear as if welded onto the larger bundles.

In any case, only two large, percurrent bundles are in evidence just below the next bracts. The departing median trace of each bract there divides each percurrent bundle into two, making four in all. However, in the next internode we find six bundles again arranged in two series, but these series at right angles to the corresponding configuration of the internode below. In the nodal area, therefore, a fusion must have taken place reconstituting a pair of percurrent bundles.

The pistillate spike of *P. pauciflorum* bears only one flower per bract. The four non-percurrent traces may fuse into two bundles soon after giving rise to the single bracteal trace, judging from a lateral view (Fig. 12c). There are four bundles discernible in a transection just below the flowers. The floral traces issue from both the median and the percurrent bundles. The latter run to well above the floral pedicles and terminate abruptly just below the aborted apical meristem. The pistillate spike can thus easily be visualized as a simplified version of the staminate one, both externally (reduction in number of flowers) and internally.

In *P. juniperinum* the staminate fertile internode is extremely short, and the floral traces radiate out from just above its base. The skeletal structure is essentially the same as that in *P. pauciflorum*, however, differing only in being greatly condensed. Except for the floral traces and the percurrent bundles which terminate in a rather broad vascular fan below the inflorescence apex, no vascular bundles are visible in the fertile internode.

Although we have already seen that *P. californicum* differs in many details of external morphology from other northern species of *Phoradendron*, it is nevertheless surprising to find its internal structure to be of such a greatly different organization. A central stele of percurrent bundles is again present in the pistillate spike. It is partly obscured, however, by a rather dense thicket of ramifying slender bundles which appears to extend throughout the cortex, forming a reticular cylinder around the central stele. This reticular cylinder is present also in the basal sterile internode of the spike (perhaps even in normal vegetative internodes?) and reaches from above the subtending bracts into the next bracts. It is visible even in the most distal portion of the spike just below the aborted apex. It ramifies also into the floral cups, but does not there from the aggregates known from *D. legelliformis*. The vein endings are slightly swollen. The entire reticular cylinder can be visualized as a three-dimensional version of the reticulum of *D. flagelliformis*. In cleared spikes one can also detect the more consistently longitudinal direction of the slender interior veins of the reticulum. Floral vasculation appears little different from that seen in other Phoradendreae.

We find thus in the few species here discussed an entirely unsuspected variation in the anatomical composition of the inflorescence. Species which usually have been regarded as closely related (*P. juniperinum*, *P. californicum*) may show great internal differences. On the other hand, a species of one genus may not differ appreciably in this regard from one of the other genus (*P. pauciflorum*, *D. costaricensis*).

We are also disappointed in our hopes to find in the anatomical construction of spikes clues to the dynamics involved in flower orientation. In *P. pauciflorum*, for example, it would be quite simple to make a "workable" model of the vascular structure if all flowers were differently oriented. In short, there appears to be no necessary relation between stelar structure and flower orientation. Here, as in the organographic aspects of this study, the very diversity of structure prohibits general morphogenetic explanations.

IV. Concluding remarks

I have frequently referred to the inflorescences of Phoradendreae as *spikes*. This is in accordance with Eichler's (1868) discussion as well as Rickett's (1955) recent definition. Eichler regarded the apical flower of a flower area as comparable to a primary lateral axis, the lateral series of the 1a and 1b types to accessory (secondary) laterals. Type 1c can easily be derived from 1b. Both types 2a and 2b fit into Eichler's hypothesis. It must be admitted, however, that inflorescence 2c provides difficulties in this regard, as the intermedian series is neither median nor lateral; it appears to represent an entirely new development.

The only doubt which, in my opinion, can be thrown upon Eichler's thesis is provided by the vascular reticulum seen in different forms in *D. biserrula*, *D. flagelliformis*, and *P. californicum*, to which can be added York's "collar traces" in *D. opuntioides* and *D. gracilis*. Could it be that in reality we are faced with a more complex inflorescence of which these reticular bundles are vestiges? Are the fertile internodes really internodes, or does each flower in reality represent a node? It seems to me that such an hypothesis has little support. Although the "collar traces" of York are said to supply the collar, there is no such exclusive relation between reticular bundles and floral cups in the species at my disposal. The facts of floral ontogeny (as far as known) and the consistently decussate phyllotaxy within spikes appear to be quite sufficient to discount any such hypothesis. I believe we have before us, in these reticular stelar proliferations, a most convincing example of a case where the vascular structure is anything but conservative. The teratological specimen of *P. dimidiatum* in Fig. 11c also lends support to Eichler's interpretation, as here a lateral axis takes the place of the apical flower, and *is supplied with prophylls*.

The inflorescence of the Phoradendreae is perhaps not as unique as it seems. Eichler already drew attention to the staminate inflorescence of *Gnetum* where the flowers also appear to arise from a ring-like intercalary meristem. VAN TIEGHEM (1896*a*) also refers to the longitudinal seriation of flowers in *Korthalsella* (Viscoideae), where we may think of one median and two lateral series of one flower each per bract. In *Notothixos* (Viscoideae), an inflorescence unit terminates in a fertile internode which has about five flowers per bract, arranged in a typical 2a fashion. To conclude on the basis of such a similarity that *Notothixos* is closely related to Phoradendreae would indeed be incautious, as evolutionary convergencies abound in the Viscoideae (see below).

We can discern in the evolution of these inflorescences, as inferred from structural details, the evolutionary processes of reduction and elaboration in action simultaneously. Surely we must regard the serial flower production and the vascular reticulum as an elaboration upon simpler situations; and just as certainly does heterophylly, and the reduction of the anther to an evascular sessile pollen sac or pair of pollen sacs indicate reduction. To single out reduction phenomena as the main evolutionary processes surely does not apply in the Phoradendreae, as the main tribal characteristic is one of elaboration (i.e. seriation of flowers).

The present work is not intended as a taxonomic study. Nevertheless, it has certain taxonomic implications. The fragmentary nature of my observations, however, precludes even a partial revision of the two genera involved.

Yet it will be advisable, in my opinion, to look at the subgeneric organization of *Phoradendron* in a manner influenced as little as possible by Trelease's treatment. I am convinced that the primary division of the genus into Boreales and Aequatoriales, even if it will turn out to be a natural one, is at least incorrectly or incompletely defined. The northerly squamate species cannot logically be placed in either subdivision, as all their scale leaves could be regarded as cataphylls. Such species as *P. calyculatum* and *P. falcatum* are nearly indistinguishable morphologically except for one pair of basal cataphylls in the latter. If *D. aequatoris* turns out to belong in *Phoradendron* (cf. footnote, p. 545) it will further embarrass the system, as the species is without cataphylls, yet can scarcely be represented as an Ecuadorian member of the Boreales! In *Dendrophthora* there is at least one species (*D. buxifolia*) which may or may not have basal cataphylls, differing in this regard even within one plant. In *Dendrophthora*, therefore, the occurrence of cataphylls does not appear to follow lines of affinity.

In his lower infrageneric organization Trelease has made a chaotic confusion between artificial keys and natural groups. He obviously regards these lower divisions as taxa, since he provides each with a formal latin name as well as with a diagnosis, and even with geographical data. Yet I think except for later nomenclatural problems these subdivisions should be regarded as nothing but portions of an artificial key. An example will support my argument. *P. jenmanii* is described (p. 85) as a member of "20.Rigidae". Yet we find it again in the key to "F. Continuae, III. Percurrentes" (p. 143) and even for a third time in the key to "IV. Dichotomae" (p. 156). In a similar way *P. obliquum* and *P. laxiflorum* can be discovered in the keys of three different subdivisions. Surely such groups cannot be held to be natural units! It is unfortunate that, because of the formal diagnosis, future nomenclature is chained to Trelease's names of these subdivisions; but taxonomic concepts should not be led astray by them.

In particular, this study has pointed out the necessity of removing *P. californicum* from the position given to it by Trelease. It differs from its sympatric species in details of phyllotaxy, inflorescence type, inflorescence anatomy, and ecological and host preferences which, taken together, make a reconsideration of its taxonomic position inevitable. Such a reconsideration is futile, however, until the entire genus can be critically revised. The position of *P. californicum* has important nomenclatural implications as it is the type species of *Phoradendron*.

If any feature is conspicuous in the previous pages it surely is the occurrence of evolutionary parallellisms, or convergent evolution, in the structure of Phoradendreae. It is one of the major aspects of orthodox taxonomy to weigh such apparently parallel developments, and to decide which coincides with natural taxonomic boundaries. It is perhaps useful, therefore, to list the most conspicuous convergences in the Phoradendreae:

1. the occurrence of basal cataphylls
2. the 1b type of inflorescence
3. dioecious and monoecious species are present in both genera
4. the position of the first pair of appendages following, and in relation to the position of the prophylls of lateral axes
5. the squamate habit
6. dichasial branching
7. reticular stelar elaborations in the spike.

In the face of these convergences which appear not to be related to taxonomic lines of affinity one naturally is reminded of the slightness of the character which distinguishes *Phoradendron* from *Dendrophthora*, namely the bilocular as contrasted to the unilocular anther. It could well be that this distinction will one day have to be abandoned; that entirely new boundaries will have to be established in accordance with several of the points listed above and that, in turn, the staminal features will come to be regarded as a convergent evolutionary character which has arisen independently in more than one group.

SUMMARY

Heterophylly is frequent in *Dendrophthora* and *Phoradendron*, and may take many forms. The concepts prophyll, cataphyll, and scale-leaf are briefly discussed and defined as to usage in the Phoradendreae. Various morphological details of patterns of heterophylly, flower orientation and seriation, fusion of prophylls, phyllotaxy, sex distribution and inflorescence position are traced as far as the available material permits. A typology of inflorescences in these two genera is proposed, based on flower seriation.

Anatomical observations on a few species of both genera have revealed striking and unsuspected structural differences between the inflorescences of some seemingly related species, but also similarities which cross the intergeneric boundary. The discovery of "extra-stelar" vascular proliferations in some species of both genera is of particular interest.

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LIST OF PHORADENDREAE REFERRED TO IN THE TEXT

(those illustrated provided with *)

DENDROPHTHORA

D. aequatoris (Urb.) Trel.
D. biseriata Urb.
D. biserrula Eichl.*
D. buxifolia (Lam.) Eichl.
D. chrysostachya (Presl) Urb.
D. clavata (Benth.) Urb.
D. constricta (Griseb.) Eichl.
D. costaricensis Urb.*
D. cupressoides (Macf.) Eichl.*
D. cupulata (DC) Eichl.
D. danceri (v. Tiegh.) Krug Urb.
D. domingensis (Spreng.) Eichl.
D. elliptica (Gardn.) Krug Urb.
D. epiviscum (Griseb.) Eichl.
D. flagelliformis (Lam.) Krug Urb.*
D. glauca (Griseb.) Eichl.
D. gracilis (DC) Eichl.
D. grisebachii Eichl.
D. lindeniana v. Tiegh.
D. nipensis Urb.*
D. opuntioides (L.) Eichl.
D. paucifolia (Rusby) Kuijt, **comb. nov.**1)*
D. poeppigii v. Tiegh.*
D. remotiflora Urb.*
D. sessilifolia (Griseb.) Krug Urb.
D. squamigera (Benth.) Kuntze
D. subtrinervis Urb.
D. ternata Urb.*
D. tetrastachya (Griseb.) Urb.*

PHORADENDRON

P. aequatoris Urb.
P. anceps (Spreng.) Gomez de la Maza
P. aureum Trel.
P. bolleanum (Seem.) Eichl.
P. brachystachyum (DC) Trel.
P. californicum Nutt.
P. calyculatum Trel.*
P. cheirocarpum Trel.
P. craspedophyllum Eichl.*
P. crassifolium (Pohl ex DC) Eichl.*
P. demerarae Trel.
P. densum Torr. ex Trel.
P. diguetii v. Tiegh.
P. dimidiatum (Miq.) Eichl.*
P. falcatum Eichl.
P. fanshawei Maguire
P. fendlerianum Eichl.*
*P. flavescens = serotinum**
P. fragile Urb.
P. galeottii Trel.
P. globuliferum Trel.
P. henslovii (Hook. f.) Robinson*
P. herbert-smithii Trel.
P. jenmanii Trel.*
P. juniperinum Engelm.*
P. laxiflorum Ule
P. libocedri cf. *juniperinum*
P. liga (Gillies) Eichl.
P. ligatum cf. *juniperinum*
P. macrophyllum (Engelm.) Cocker.*
P. martianum Trel.
P. minutifol'ium Urb.
P. obliquum (Presl.) Eichl.
P. paradoxum Urb.*
P. pauciflorum Torr.*
P. paucifolium = Dendrophthora
P. piperoides (HBK) Trel.*
P. platycaulon Eichl.*
P. polygynum (Karst.) Eichl.
P. quadrangulare (HBK) Krug Urb.
P. racemosum (Aubl.) Northrop
P. robinsonii Urb.
P. scaberrimum Trel.
P. serotinum (Raf.) M. C. Johnston*
P. surinamense Pulle
P. tlacolulense Loes.
P. tomentosum (DC) Gray
P. tonduzii Trel.*
P. tunaeforme (DC) Eichl.
P. uspantanum Trel.
P. velutinum (DC) Trel.
P. villosum (Nutt.) Engelm.
P. wattii Krug Urb.

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1) *Phoradendron paucifolium* Rusby, Bull. N.Y. Bot. Club **6**: 510. 1910. This recombination has apparently never been made. The isotype at UC (WILLIAMS, 1530) shows it to be closely related to *D. squamigera*, and I therefore do not hesitate to make the transfer although I have not seen the anthers (cf. Fig. 5).

LITERATURE CITED

Eichler, A. W. 1868. Loranthaceae, *in* Martius, Flora Brasil. **5** (2).

Fosberg, F. R. 1941. Notes on Mexican plants. Lloydia **4** (4): 274–290.

Goebel, K. 1932. Organographie der Pflanzen. 3*d* ed. **3**: 1603–1609. Jena.

Jackson, B. D. 1949. A glossary of botanic terms. London.

Johnston, M. C. 1957. *Phoradendron serotinum* for *P. flavescens* (Loranthaceae): nomenclatural corrections. Southw. Natural. **2** (2/3): 45–47.

Johnson, T. 1888. *Arceuthobium oxycedri.* Ann. Bot. **2**: 137–160.

Karsten, H. 1859. Flora Colomb. **1** (2): 73–74, Plate 36.

Kuijt, J. Morphological aspects of parasitism in the dwarf mistletoes (*Arceuthobium*). Univ. Calif. Pub. Bot. (in press).

Maheshwari, P., B. M. Johri and S. N. Dixit. 1957. The floral morphology and embryology of the Loranthoideae (Loranthaceae). Jour. Madras Univ., B, **27** (1): 121-136.

Mekel, J. C. 1935. Der Blütenstand und die Blüte von *Korthalsella dacrydii.* Blumea **1** (2): 312–319.

Rickett, H. W. 1954. Materials for a dictionary of botanical terms. I. Bull. Torr. Bot. Club **81** (1): 1–15.

———. 1955. Materials for a dictionary of botanical terms. III. Inflorescences. *Ibid.*, **82** (6): 419–445.

Smith, F. H. and E. C. Smith. 1943. Floral anatomy of the Santalaceae and some related forms. Oregon State Monogr., Stud. in Bot., No. 5.

Tieghem, P. van. 1896*a*. *Korthalsella*, genre nouveau pour la famille des Loranthacées. Bull. Soc. Bot. France **43**: 83–87.

———. 1896*b*. Sur le groupement des espèces et genres dans les Ginalloées, Bifariées, Phoradendrées et Viscées, quatre tribus de la famille des Loranthacées. *Ibid.*, **43**: 161–194.

Trelease, W. 1916. The genus *Phoradendron.* Urbana, Illinois.

Tubeuf, K. von. 1923. Monographie der Mistel. Berlin.

Urban, I. 1896. Ueber die Loranthaceen-Gattung *Dendrophthora* Eichl. Ber. Deut. Bot. Ges. **14**: 284–294.

———. 1897. Plantae novae americanae imprimis Glazioviana. I. Loranthaceae. Bot. Jahrb. **23** (5): 1–16.

Wardlaw, C. W. 1952. Phylogeny and morphogenesis. London.

York, H. H. 1913. The origin and development of the embryo sac and embryo of *Dendrophthora opuntioides* and *D. gracile.* I and II. Bot. Gaz. **56**: 89–111, 200 216.

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PALYNOLOGY OF THE "UDDELER MEER"

A CONTRIBUTION TO OUR KNOWLEDGE OF THE VEGETATION AND OF THE AGRICULTURE IN THE NORTHERN PART OF THE VELUWE IN PREHISTORIC AND EARLY HISTORIC TIMES

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(*received July 3rd*, 1959)

INTRODUCTION

In 1948 VAN ZINDEREN BAKKER published a paper entitled "Palynological and Stratigraphic Research on Bogs on the Veluwe", in which an account is given of most of the bogs found in that part of the country, and in which the "Uddeler Meer" too is dealt with. With regard to this sheet of water the author says that he obtained the impression that the deposits showed a pollution due to human activities. He also studied the "Bleeke Meer", 1 km to the north of the "Uddeler Meer", where he obtained a series covering the Preboreal and Boreal periods.

As VAN ZINDEREN BAKKER had taken his samples only along the banks of these sheets of water, the present author thought that it would be worth while to extend the investigation to deposits found in the centre of the latter. Thanks to the kind cooperation of Messrs Ir. E. Reinders and Ir. A. J. Lanz, who have the supervision of the Royal Crown Lands as foresters of this area, she could make use of a raft belonging to the swimming pool situated in the "Uddeler Meer", and move it to various parts of the latter. Sampling was done from this raft by means of a Dachnowsky auger. In this way she could sample 4 m of the organic mud under a cover of circ. 2.45 m water.

The "Bleeke Meer" originally was filled with peat; in fact, it derived its name ("bleek" means pale) from the *Young Sphagnetum* which formed the uppermost layer. The peat has been removed, only a small island being left, and on the latter the entire deposit down to the subsoil was sampled. The "Bleeke Meer" started with the same sediment and at the same time as the "Uddeler Meer", but being less deep, the mud became in due time covered with peat. Records of the "Bleeke Meer" will be published at a later date.

SITUATION AND ORIGIN OF THE "UDDELER MEER" AND OF THE "BLEEKE MEER"

The two sheets of water are situated in an outwash plain between two sand ridges (Fig. 1); to the north and to the south inland dunes occur. As the map (Fig. 1) shows, the region is very poor in surface water; (the sheets of water in the northern part are remains of the former Zuiderzee, which originated from a transgression of the North Sea in early historic times). A hundred years ago the area was entirely covered with heather; nowadays there are still large stretches of heath, but a great part of the latter has been reclaimed or has been planted with pine.

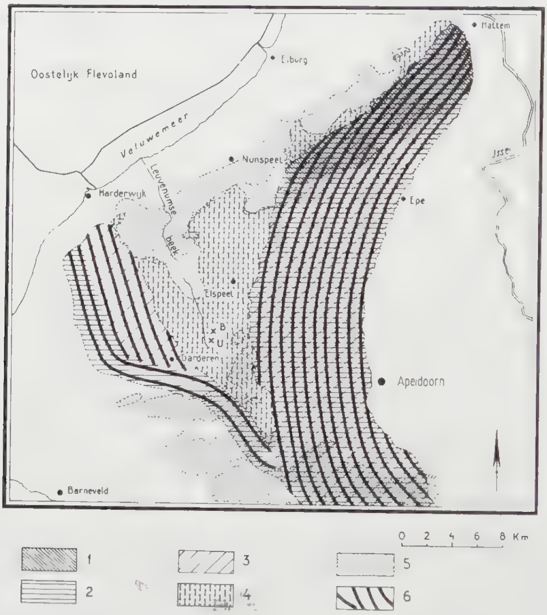


Fig. 1. Geomorphological map of the northern Veluwe. (after Maarleveld)
1, 2, 3, 6: Ice pushed ridges
4 : Outwash plain
5 : Inland dunes
U : Uddelermeer
B : Bleeke Meer

Until a short time ago geologists assumed that both sheets of water are Sölle or pseudo-Sölle (kettle-holes), i.e. that they originated either from dead ice of the Riss period or from holes blown out by the wind during the Younger Dryas period. Lorie (1910) considered the "Uddelermeer" as a deep scour hole in a bend of a Fluvioglacial river. Recently, however, Maarleveld (1955) came forward with another interpretation. According to him, these circular depressions in the landscape are remnants of pingos dating from the Würm Glacial period. Such a pingo owes its origin to the hydrostatic pressure of the ground water, and the crystallization force of ice. This causes faults with the result that the ice mass comes to the surface where it partly melts during the summer, the water running down the slopes in the form of rivulets. The pingo therefore is enclosed by a crater-like ridge. Depressions of this kind occur nowadays in regions with a permanently frozen subsoil, and such a permanently frozen subsoil was present in the Netherlands during the Würm Pleniglacial period.

The ridges round the "Uddeler Meer" and the "Bleeke Meer" are rich in gravel. The eastern part of the bank of the "Uddeler Meer" has been heightened artificially; this is the horseshoe-shaped "Hunneschans" (Fig. 2), which dates from the first centuries of our era.

In both sheets of water the sedimentation of organic mud started in the Older Dryas time, which is in accordance with the conception that they came into existance in the Würm Pleniglacial period.

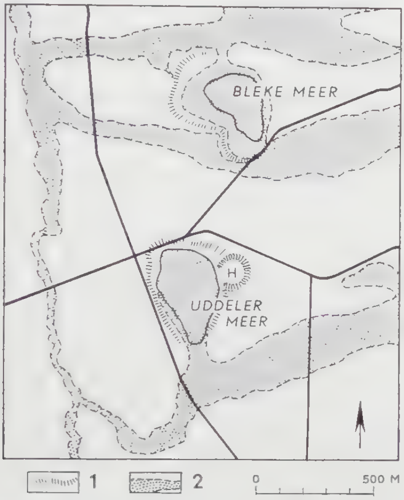


Fig. 2. Map showing the shapes and also the ridges around "Uddelermeer" and "Bleeke Meer". (after Maarleveld)

1: Ridges
2: Valleys and depressions filled with residual material
H: Hunneschans

Methods

As mentioned before, sampling was done with a Dachnowsky auger from a raft and under a water layer of circa 2.45 m. The deeper layers of the deposit are rather stiff and dry, but upwards the mud becomes thinner and thinner and finally it becomes so thin that the youngest deposits could not be sampled. All the samples contain drift sand, especially at the bottom and at the top. Van Zinderen Bakker (1948) mentions the presence of erratic sandgrains in the greater part of the samples he obtained from different localities on the Veluwe. He comes to the conclusion that sanddrifts occurred there throughout the whole Post-Glacial period.

The material was treated with HF, acetolysed and stained with fuchsin. Counting was done with Zeiss Neofluar objectives, which give very clear pictures. For difficult pollen identifications a phase-contrast immersion-objective was used, with the help of which the genera of the cereals could be determined.

Since the work of Firbas (1937) it has become possible to distinguish the pollen of cereals from that of wild grasses. *Secale cereale* in most cases could be set apart by its shape, but *Triticum*, *Hordeum* and *Avena* originally were undistinguishable. With the phase-contrast method it turned out that there is a marked difference in sculpture. *Hordeum* often has an undulated contour, the small granules on the surface being rather wide apart. In *Triticum* the granules are arranged in an irregular pattern, and several of them are fused. In the annulus large dark spots occur which owe their origin to such fused granules. *Avena* again has a regular pattern with large granules. In *Secale* too the arrangement of the granules is regular, but the latter are very minute. The same minute granules occur in *Elymus arenarius*, but here they are wider apart; as in other large pollen grains from wild grasses, the cell wall is thinner than in the cereals, and the annulus also is thinner and less protruding.

When I had nearly completed my manuscript, I became acquainted with an article by Udelgard Grohne (1957) in which she describes similar observations, and in which the different patterns of sculpture are illustrated by clear pictures. She also distinguishes the shape and pattern of the annuli, and indicates how the pollen of wild grasses can be distinguished from that of cultivated ones.

In order to obtain a clear insight into the changes which took place in the vegetation, several hundreds to over a thousand grains of arboreal pollen were counted pro sample, and most of the non-arboreal pollen grains were indentified too. The textbook of Faegri and Iversen (1950) and a rather extensive collection of recent pollen grains proved indispensable.

The zonation of Jessen as described in the textbook mentioned above, is applied here.

STRATIGRAPHY

At four places samples were taken. The main section is represented in Diagram I, and the three additional ones may serve to complete the image created by first one. Diagram I covers the main part of the series, from Dryas I to the Subboreal period. Sections (diagrams) II and III were sampled to obtain more details with regard to the bottom layers. The sedimentation started in the Older Dryas time, but a Bølling oscillation could not be detected. Diagram VI and VII are from the more recent layers. The deposits gradually become very thin; they could nevertheless be sampled up to the Subatlanticum.

In future more details will be given with regard to samples obtained from below the deepest point of the "Uddeler Meer", which was found after the other sections had already been investigated. In the "Bleeke Meer" a very fine Late-Glacial mud was found; in this mud the Allerød layer shows a sharp contrast in colour with the sediments of the two Dryas times.

All the sediments of the "Uddeler Meer" were deposited in water; they contain besides pollen and spores, plankton *Algae*, fragments of aquatic *Crustaceae* and other animal residues.

In section I, below a depth of 6.20 m the subsoil could not be penetrated by the auger. It consists of a very coarse gravelly sand. Up to approximately 4.90 m the sediment is a gyttja; from there on it changes gradually into a dark brown dy. Especially the Late-Glacial samples have a greenish-grey colour, and contain lime. The colour caused by the presence of *Chlorophyceae*, shines as a green haze through the grey or brown. In the Allerød layers the primary colour is olive, which in Zone III again grows paler, although the green undertone persists. Lime disappears already in the Allerød.

The transition of gyttja into dy is very gradual, so that in Zones VI–VII the colour of the sediment and also of its KOH extract becomes dark brown.

Description of Section (Diagram) I

Nrs 1–3

Olive-green; *Cladocera*, *Protococcales*, colonies of *Cyanophyceae* (*Gloeotrichia?*), *Hypnaceae*.

No 4

Colour brownish; more *Hypnaceae* than in 1–3.

Nrs 5 and 6

Greenish; *Cyanophyceae* (*Gloeotrichia*?), less *Hypnaceae*

Nrs 7–10

Cyanophyceae, less *Cladocera*, less *Hypnaceae*

No 11

Radicels and epiderms of Monocotyledons, *Hypnaceae*, *Cyanophyceae*

No 12

Hypnaceae, one leaf of *Sphagnum*, radicels, epiderm of *Gramineae*, no *Cyanophyceae*, *Pinnularia* (250 μ)

No 13

Radicels, *Hypnaceae*, microphyllous *Sphagna*, div. species of diatoms (*Navicula*)

No 14

Radicels and epiderms of *Cyperaceae*, shells of *Cladocera*, mandibles of *Arthropoda*, *Hypnaceae*, microphyllous *Sphagna*, leaf fragments of Dicotyledons (*Betula*?), woodvessels of *Betula*, some diatoms (*Navicula*)

No 15

Same as 14, but with *Rhizopoda* (*Centropyxis* type)

Nrs 16 and 17

Radicels and epiderms of *Cyperaceae; Hypnaceae* and microphyllous *Sphagna; Cladocera* shells; mandibles of *Arthropoda;* diatoms rather abundant

No 18

Radicels and epiderms of *Gramineae* and *Cyperaceae; Hypnaceae* and microphyllous *Sphagna;* leaf fragments of Dicotyledons; *Cladocera* and mandibles of *Arthropoda;* diatoms (*Pinnularia* and smaller species)

Nrs 19 and 20

Rather coarse, with much detritus; radicels, *Hypnaceae* and microphyllous *Sphagna*, woodvessels *Betula*, diatoms

No 21

Same, but with more diatoms (*Pinnularia*)

Nrs 22 and 23

Same, but with less diatoms

No 24

Same, but with few diatoms; spiculae of *Spongilla;* radicels and epiderms abundant (*Phragmites*); hairs of *Nymphaeaceae;* needle leaf of *Pinus;* animal remains

No 25

Fibrous; vessels, epiderms, humus flocks, few *Cladocera*, charcoal, some *Hypnaceae*, *Cenococcum geophilum*

No 26

Same; *Cyanophyceae* rather abundant, spiculae of *Spongilla*, diatoms

Nrs 27, 28 and 29

Less fibrous, flocks of humus; *Cyanophyceae*, more *Hypnaceae*, more *Cladocera*, mandibles of *Arthropoda,* spiculae of *Spongilla*, charcoal, *Cenococcum*

Nrs 30 and 31

Same, but more diatoms and less *Chlorophyceae* and *Cyanophyceae; Thelypteris* sporangium filled with spores, moss sporangium, *Microchaete*? (*Cyanophyceae*)

No 32

Detritus and humus, radicels, *Cladocera*, sporangia and setae of *Hypnaceae*, charcoal, *Microchaete*?, hairs of *Nymphaeaceae* + +, spiculae of *Spongilla*

No 33

Same, more *Spongilla*

No 34

Same; oospores of *Chara* —, *Cladocera* and other *Arthropoda* +, setae and sporangia of *Hypnaceae*, petioles of *Ceratophyllum* with hairs, hairs of *Nymphaeaceae*, *Microchaete*?, *Spongilla* and diatoms

No 35

Less *Chara*, *Cladocera* + +, *Ceratophyllum* + +, Radicels —, setae and sporangia of *Hypnaceae*, hairs of *Nymphaeaceae*, *Spongilla* and diatoms

No 36

Radicels and epiderms —, *Chara* spores ±, setae and sporangia of *Hypnaceae* +, *Cladocera* ±, *Copepoda*, *Cyanophyceae*, charcoal, diatoms (*Pinnularia*), *Spongilla* ±, *Ceratophyllum* hairs—, *Cenococcum.*

No 37

Same, but with less diatoms and *Spongilla.*

No 38

Chara spores ±, setae and sporangia of *Hypnaceae* —, *Cladocera* + *Cyanophyceae* (*Microchaete*?), charcoal, diatoms —, *Spongilla* —, *Ceratophyllum* petioles and hairs +, *Cenococcum*, clusters of *Phycomycetes*

Nrs 39–41

Same with microphyllous *Sphagna*, radicels ±, less *Ceratophyllum*, *Nymphaea* hairs

Nrs 42–44

Same, but without *Microchaete*?

Nrs 45–50

Larger residues very scarce, humus flocks, no *Ceratophyllum; Ostracoda*, *Copepoda*, *Cladocera*, further as 42–44

Section II (Diagram II)

As in Section I the subsoil consists of coarse gravelly sand, rich in lime. It is situated at a depth of 6.00 m. The first sample taken at a depth of 5.97 m is still very sandy and contains hardly any pollen. Incrusted *Chara* oospores occur together with a network of fungal hyphae and large fungal sporangia.

No 2

Same as No 1, with fruit of *Carex* and seta of a *Hypnacea*

No 3

Finer sand, high content of lime; incrusted *Chara* oospores +, *Cladocera, Arthropoda,* fruit of *Carex, Hypnaceae* ±

No 4

Same, less mossess

No 5

Same, less mosses, less *Chara*

Section III (Diagram III)

Subsoil at 6.20 m, the same as in Section I and II. Samples 2 and 3 with hardly any pollen but containing a network of fungal hyphae and sporangia

No 4

Transition to organic sediment: incrusted *Chara* oospores +, *Cenococcum geophilum*, *Cladocera* and other animal residues +, rhizomes and radicels, *Cyanophyceae*,

Nrs 5 and 6

Fine sediment, ca 80 % of lime; the same as No 4, *Hypnaceae* +

Section IV (**Diagram VI, VII**)

The first samples are very wet, semi-fluid. The colour is pale green caused by clusters of *Algae*, such as *Scenedesmus*, *Tetraedron*, *Pediastrum* and *Botryococcus*. Microphyllous *Sphagna* occur, sporangia, setae and leaves of *Hypnaceae*, *Cladocera* and *Tubifex*

Nrs 3 and 4

Hypnaceae, microphyllous *Sphagna*, epiderms and radicels, megaspores of *Isoetes lacustris*, *Chara* oospores, fruits of *Potamogeton natans* and other *Potamogeta*, *Nymphaea* seed, sporangia of *Fungi*, *Cladocera*, *Tubifex* and mites.

No 5

Same, more radicels and epiderms

Nrs 6 and 7

Same, radicels and epiderms +, fruits of *Potamogeton natans*, *P. obtusifolius* and *P. acutifolius*

No 8

Balls of detritus, radicels, epiderms, megaspores of *Isoetes lacustris*, setae, leaves, sporangia of *Hypnaceae*, *Chara* oospores, *Nymphaea* hairs, sporangia of *Fungi*, *Cladocera*, *Tubifex*, *Rhizopoda* + (*Nebela* spec.?)

No 9

Same, but without *Rhizopoda*

No 10

Same, *Rhizopoda* ++ (*Nebela* ?)

THE DIAGRAMS

LATE-GLACIAL (Diagrams I, II, III; Tables I, II, III, IV). As mentioned before, the sub-soil of gravelly sand is rich in lime, and it contains abundant oospores of *Chara*. With the exception of fungi, other organic remains are scarce. The texture of the sand is represented in Table I.

TABLE I

Granular Composition of Subsoil at 6–6.70 m.

Larger than:	420	300 – 420	210 – 300	149 – 210	105 – 149	74 – 105	53 – 74	53 – 53	2 16	2 μ
Number 1	16.6	18.	19.4	15	7.2	0.8	8.7	11.7	0.7	1.9 %
Number 2	12.6	11.8	15.7	16.7	12.1	3.5	11.8	11.5	1.4	2.9
Number 3	10.7	28.9	37.4	11.7	6.4	0.4	1.5		3.0	

The "Uddeler Meer" must have started as a hard water pool in which the vegetation was poorly developed and in which *Chara* dominated. Judging from the pollen no phanerogamic marsh or water plants were present, but *Cyperaceae* are well represented, and come next to the *Gramineae*. Striking is the relatively high percentage of liguliflorous *Compositae*; this pollen strongly resembles that of *Taraxacum* (WODEHOUSE, 1935). GODWIN (1956) mentions finds of fruits of the latter from the Full and Late-Glacial and from the early Post-Glacial

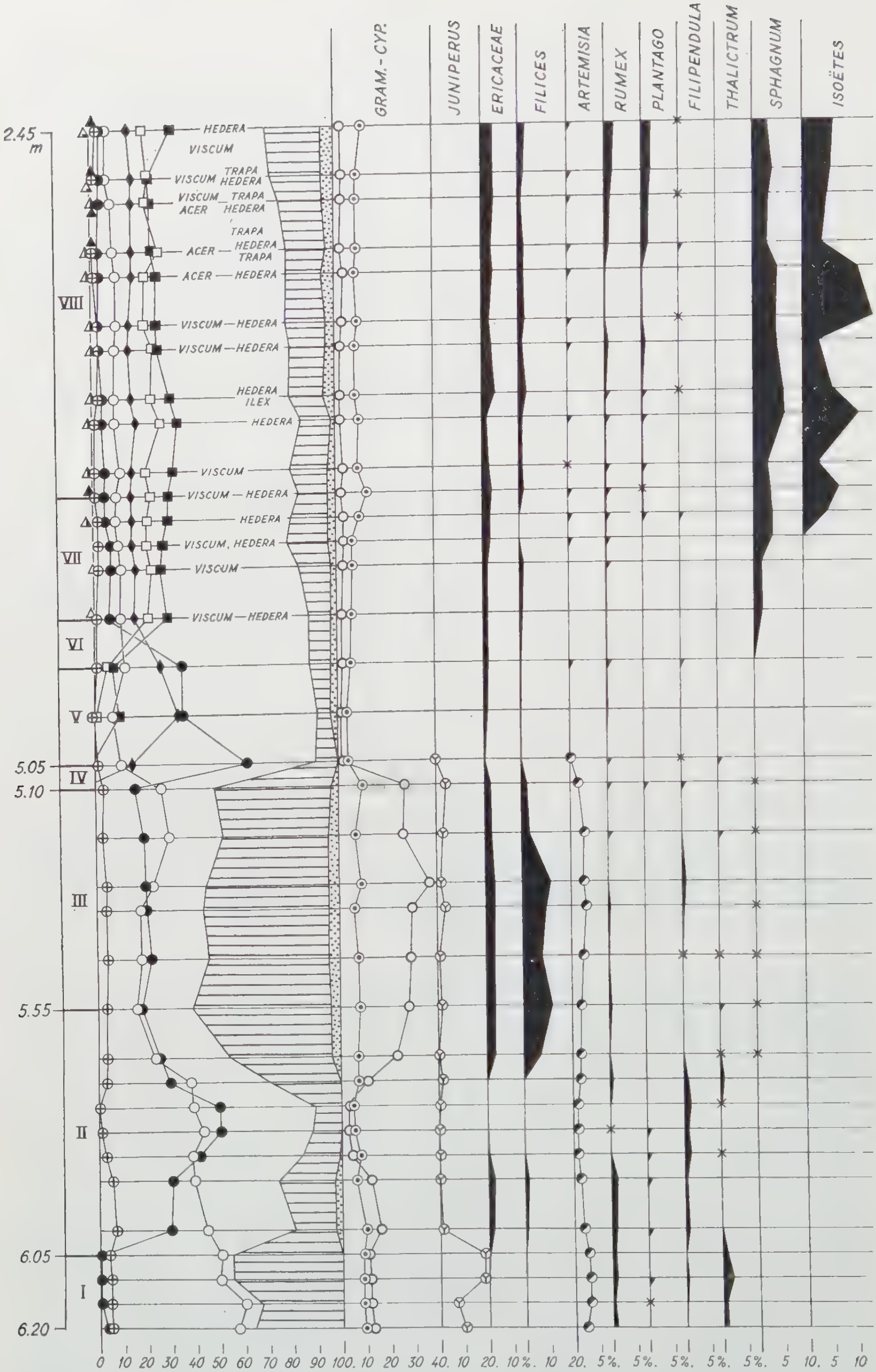
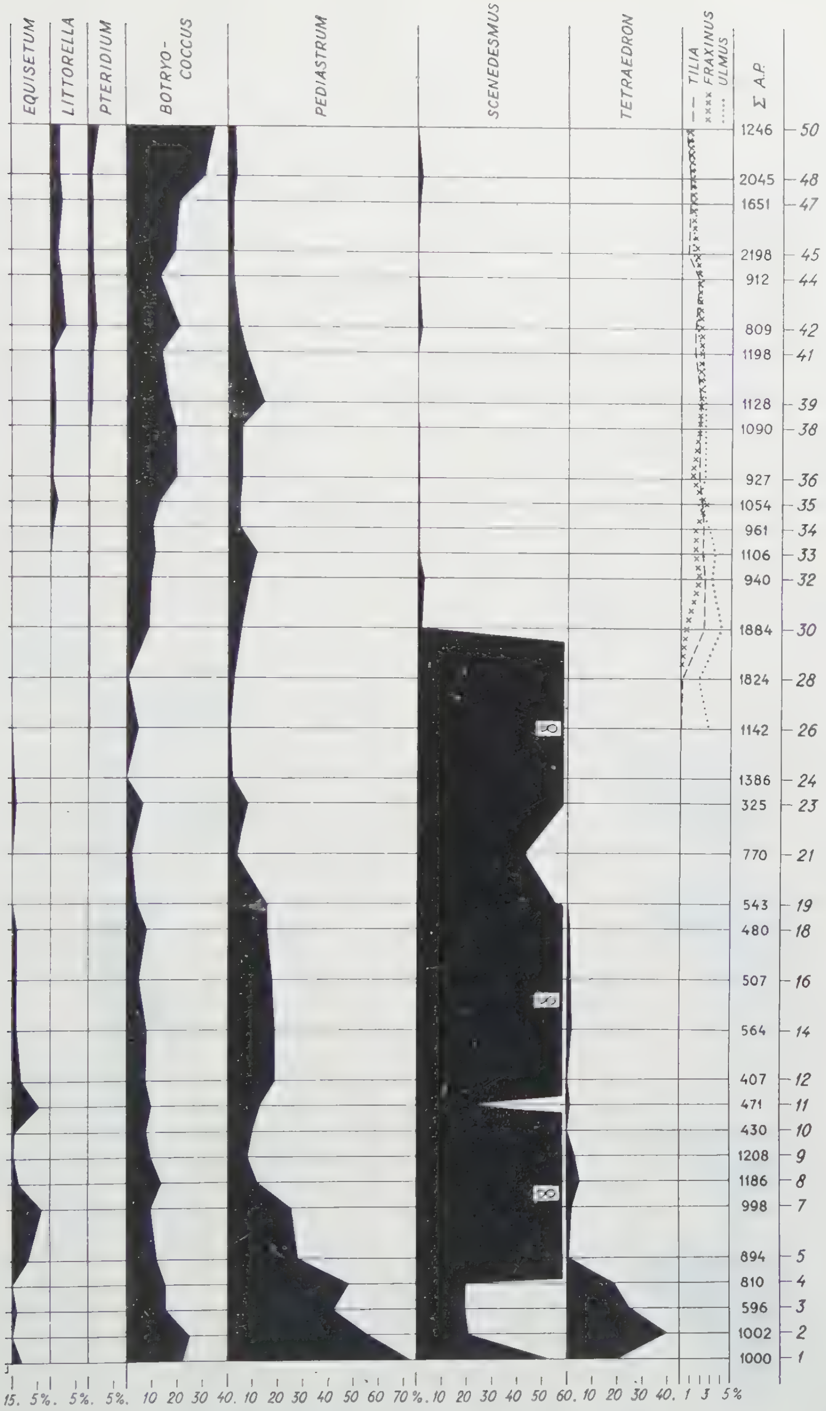


DIAGRAM I

Section through Late-Glacial and Post-Glacial deposits. Total diagram in which only pollen of aquatic plants is left out of the pollen sum.

x) single grain, found after counting.



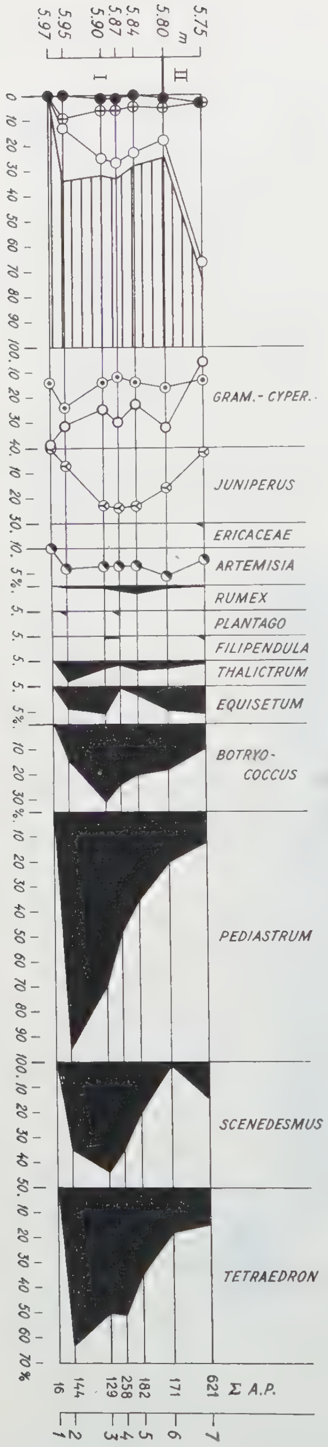
KEY TO THE SYMBOLS

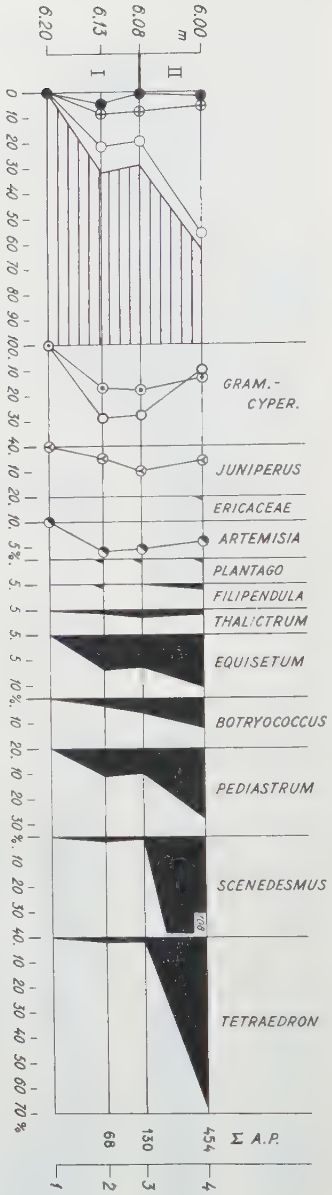
● Pinus
◆ Corylus
△ Carpinus

○ Betula
■ Q.M.
⊙ Gramineae

⊕ Salix
△ Picea
○ Cyperaceae

☐ Alnus
▲ Fagus
▨ Ericaceae





DIAGRAMS II and III
Late-Glacial; Dryas I and beginning of Allerød. Note the relatively high values for *Artemisia*, *Juniperus* and *Chlorophyceae*.

					Helianthemum			Sanguisorba									Polygonum					Ranunculaceae		Rosaceae		Potamogeton						Compositae				
	Populus	Hippophaë	Cornus Sanguinea	Cornus suecica	nummularium	oelandicum	Saxifraga oppositifolia	officinalis	minor	Menyanthes	Myriophyllum spic.	alterniflorum	Epilobium	Valeriana	Lonicera	Convolvulus	amphibium	bistorta	persicaria	Galium	Batrachium	Ranunculus	Caltha	Potentilla	Geum	Eupotamogeton	Coleogeton	Chenopodiaceae	Urtica	Humulus	Umbelliferae	Tubuliflorae	Liguliflorae	Papillionaceae	Lotus	Solanum dulcamara
50			1											1					x	10		1		3	3	8	3	1			2	5	1			1
48																2				2		14		5	3	5	5	5	3		1	5	4		2	1
47															1					1		2		3	3	5	2	4	2		3	5	4		1	3
45																			1			16		3	6	4	2	3	2		2	1	1		2	
44										1									x			1			1	3		2	1		x		2	x		
42												x										1		1	2	1	3	1	1						1	
41																			x	1		2		1		3		2		x			1	1		1
39																			x		1				4	2		5	1		1	2	1	x	1	
38										x										x		1		2	1	1		3	1		x	1			1	
36																																				
35																																				
34																																				
?																																				

in England and supposes that this plant was frequent at that time because of the open soil conditions. Its next more or less accurately dated appearance in England is in Roman time. In the "Uddeler Meer" too, pollen of the same *Taraxacum* type came back in the youngest layers of the Subatlanticum (1.6 % of the arboreal pollen). In Brouwer's (1949) diagrams from Drente very high percentages for the *Compositae* are recorded, whilst Havinga in an unpublished diagram of a soil series obtained on the bank of the "Uddeler Meer" found also extremely high values for this type of pollen. However this may be, the samples obtained from deposits just above the mineral subsoil show signs of pollen corrosion, and it might be that selective corrosion plays a role in the composition of their spectra.

The samples from the higher strata are in better condition; they contain undamaged pollen and large amounts of *Chlorophyceae*. The matrix is a calcareous gyttja, grey in colour with a green shimmer, which darkens when exposed to the air.

The lower part of Diagram I, II and III (resp. samples 1–5; 3–5 and 4–6) belong to the Older Dryas time, Zone I according to Jessen and Iversen (1950). The ratio of non-arboreal pollen amounts respectively to 36–45 % 73–78 %; and 67–71 %, *Juniperus* included. A Bølling oscillation could not be distinguished in either of the three diagrams; possibly the sedimentation started in phase Ic, i.a. after the Bølling oscillation.

Dryas I (Diagram I, II, III, Zone I). A characteristic feature of Dryas I in our diagrams is that the *Juniperus* curve attains a maximum (over 20 %) in this period, in contrast to the *Juniperus* curves published by Iversen (1954) for Denmark, and by Zagwijn (1952) for the Alps, which have their maxima at the close of Zone III. These maxima, moreover, are much higher. In the records of Van der Hammen (1951), however, *Juniperus* is well developed in Dryas I and, except in Usselo c where hardly any difference between the two Dryas layers is to be seen, it reaches a maximum in the Older Dryas period. It seems probable that the Netherlands diagrams in this respect differ from the Scandinavian and the alpine ones.

Pinus stays low in Zone I, *Betula* being the main component of the tree pollen. It could not be established whether the latter originated from dwarf birches or not, but according to the characteristics of the pollengrains, Terasmaë (1951), a certain percentage may have been produced by *Betula nana*.

Salix amounts to 6 %, in one case to 8 %; the *Artemisia* curve is well-developed; it rises to over 5 %. *Rumex*, *Plantago*, *Filipendula*, *Equisetum* and ferns are represented in the diagrams, the main producers of the non-arboreal pollen, however, are grasses and sedges, the *Cyperaceae* attaining the highest values. No curves were drawn for *Helianthemum*, *Sanguisorba*, *Menyanthes*, *Populus* and *Hippophaë*. The numbers of grains found in each spectrum (a few pro mille only) are recorded in Tables II, III and IV. *Equisetum* is left out of the pollen sum.

The Allerød period is well-developed; it can be distinguished by the naked eye because of its dark colour, which contrasts with the paler samples of Dryas I and II. Right at the beginning lime disappears. There is a sharp rise in the arboreal pollen; first of *Betula*, then of *Pinus*; the non-arboreal pollen falls to 10.7 %. *Cyperaceae* retreat, and are surpassed by *Gramineae*; *Empetrum* starts with a few per cent; *Juniperus* decreases and so does *Artemisia*.

The *Betula-Pinus* forests must have been rather dense; in our area it is characteristic that *Pinus* surpasses *Betula* in the second half of the period; at this time it must have grown near the bank as *Pinus* stomata are found regularly in the samples (Table II).

Dryas II (Diagram I, Zone III)

As mentioned before, the sediments of the Younger Dryas period are pale in colour and free of lime. The rise in the non-arboreal pollen, in which *Cyperaceae* predominate, is sharp. (maximum N.A.P. 61 %). *Empetrum* shows a continuous curve with a maximum of 3.9 %; a few grains of *Calluna* and *Vaccinium* occur too. *Pinus* reaches higher maxima than in Zone I; *Juniperus* stays low, but *Artemisia* rises again. *Rumex* and *Thalictrum* show continuous curves with low values; *Plantago* and *Filipendula* become rare. *Helianthemum*, *Sanguisorba*, *Menyanthes* occur in a few pro mille, *Hippophaë* is absent and *Populus* disappears in the upper samples.

Filices show a marked rise in this period. Their frequency shows a continuous curve with a maximum of 12 %. The kidney-shaped, pitted but naked spores could be identified as belonging to *Dryopteris linnaeana*. Being a terrestrial fern, it is included in the pollen sum.

Some rare species in zones I, II and III (Tables II, III and IV).

Centaurea cyanus was not found in our samples, but of *Centaurea scabiosa* a single grain occurred in Zone I. Iversen (1954) mentions it for Zones I and III.

Cornus suecica, Zones I and III. This species was first mentioned by Van der Hammen (1951), and it is also recorded by Straka (1952, 1954) from the Eiffel where it was found in Zone III. In the Netherlands this species still occurs as a relic.

Circaea (probably *alpina*). One grain in Zone I. *C. alpina* nowadays has a wide northern range (Hulten, 1950). Lang (1952) mentions a find from the Late-Glacial of southern Germany.

Saxifraga oppositifolia, Zone I and the beginning of Zone II. Iversen (1954) found this species in different places in Zones I and III. It is mentioned by Godwin (1956) from the Full-Glacial near Cambridge and from Late-Glacial deposits in Ireland, and by Göttlich (1955) from Zone Ia of the Federsee.

Parnassia, Zone I; mentioned by Van der Hammen (1951) for all zones of the Late-Glacial.

Oxyria, Zone I; reported by Van der Hammen (1951) from Zones I, II and III.

Polygonum bistorta (*viviparum*, Hedberg, 1946) Zone I; mentioned by Van der Hammen (1951) and by Iversen (1954) for Zone III.

Polemonium, beginning of Zone II; for the Netherlands the first find was recorded by VAN ZEIST (1955) for Haule, Zone I. In England it has according to GODWIN (1956) a wide-spread Late-Glacial range; IVERSEN (1954) mentions this species for Jutland in Zone III.

Ephedra distachya, Zone II. This species was mentioned for the first time by IVERSEN (1951) as one of the steppe elements of the Late-Glacial. Since then it was found to be widespread all over Late-Glacial Europe.

GRASSES

In all our Late-Glacial spectra we found a few grains of grass pollen with a diameter of approximately 40 μ or more, which cannot be of cereals as in many cases the wall is too thin and as the pore is not sufficiently prominent. FAEGRI (1940) mentions the same kind of grass pollen from Jaeren, but there it seems probable that it belonged to *Elymus arenarius*. This, however, cannot apply to STRAKA's finds in the Eiffel (1952) nor to LANG's finds in south western Germany. The "Uddeler Meer" too was situated far from the sea shore, and therefore it seems highly improbable that *Elymus arenarius* may have occurred there in the Late-Glacial. The pollen might have been from *Glyceria* or, as the characteristics of grass pollen are not yet well investigated, from some arctic species to which till now no attention has been paid. STRAKA (1952, 1958) supposes that the large grains were produced by polyploid wild grasses. If this be so, then it remains unexplained why the grasses only showed a tendency towards polyploidy during that period. It is not known that other plants produced larger pollen-grains in the Late-Glacial.

ALGAE

Large quantities of *Chlorophyceae*, viz. *Pediastrum*, *Scenedesmus*, *Tetraedron* and *Botryococcus* colour the deposit. The numbers have been counted and are recorded in the diagrams. The counting, however, is not very accurate; *Tetraedron* and *Scenedesmus* are very small and can hardly be stained, so that a considerable percentage may have been overlooked. *Botryococcus* colours very deeply, but the large clusters often are broken up, and in this way here too counting is made difficult; to a lesser degree this applies also to *Pediastrum*.

The following species occur in the Late-Glacial: *Pediastrum boryanum* f. *longicorne Reinsch* and f. *undulatum Wille*, *P. duplex Meyen* f. *rugulosum Raciborski*. and *P. integrum Nägeli f. granulata Raciborski*. *Scenedesmus bijugatus* is abundant and *Sc. quadricauda Turpin* rare, *Tetreaedron muticum* (A. Br.) is not so abundant as *T. minimum* (A. Br.) *Hansgirg f. scrobiculatum Lagerheim.*¹) In the diagram the different species are treated as one. *Cyanophyceae* colonies of *Gloeotrichia*(?) are abundant in Zone I and occur also in II and III, but have not been recorded.

As may be seen from Diagram I, II and III, *Tetraedron* attains a high frequency in Zone I and falls sharply to low values recorded for the Zones II and III, whereas the other *Chlorophyceae* maintain high values.

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¹) Identification of *Algae* with: PASCHER, Süszwasserflora Deutschlands.

POST-GLACIAL (Diagrams I, IV, V, VI and VII; Tables II and V)

It is customary to make a total diagram of the Late-Glacial, in which both trees and herbs are taken into the pollen sum, and the percentages of tree and non-tree pollen are drawn opposite each other to give an idea of their ratio. In the diagrams I and VI we have continued the total diagram into the Post-Glacial, in order to illustrate the effect of deforestation.

Diagrams IV, V and VII are dissolved classical diagrams made of the same section. Diagram V is a "reduced" one; before adding them to the tree-pollen sum, the values found for *Alnus*, *Betula*, *Pinus* and *Corylus* have been divided by four, as it is supposed that they produce approximately four times as much pollen as the other tree genera do. In this way an attempt is made to give a picture of the part played by the different tree genera in the composition of the forest (FAEGRI and IVERSEN 1950). In all diagrams *Corylus* is included in the pollen sum.

PREBOREAL (Zone IV, Diagram I).

Zone IV is hardly developed: N.A.P. falls to 9.7 %; of the thermophilous trees *Quercus* is represented by 0.4, resp. 0.5 % [1]), *Ulmus* and *Alnus* are very low; *Corylus* comes to 15, resp. 17.1 % and *Pinus* rises sharply to 62, resp. 69 %. *Gramineae* surpass the *Cyperaceae*; *Pediastrum* falls to low values, *Botryococcus* is low, but *Scenedesmus* retains very high values. *Cyanophyceae*, especially *Gloeotrichia*(?), are rather abundant; star-shaped colonies consisting of *Gloeothece*-like cells also occur. A few pollen grains of Late-Glacial species are met; *Sanguisorba minor*, *Selaginella* and *Botrychium lunaria* are still present.

BOREAL (Zone V and VI, Diagram I, IV, V)

In this section first *Pinus* and soon afterwards *Corylus* reaches distinct maxima. In the sediment *Pinus* stomata occur in fair amounts; this is therefore the second period in which *Pinus* grew near the bank. Allerød and Boreal are the only periods in which *Pinus* was an important component of the forest.

Ulmus starts with 3.2, resp. 3.4 %, *Quercus* with 6.5, resp. 7 %. *Tilia* rises in Zone VI from a few pro mille to 2.4, resp. 2.8 %. *Calluna* comes to 1.7, resp. 1.8 %; the N.A.P. ranges from 8 to 11.7 %.

Towards the end of the Boreal oligotrophic waterplants begin to immigrate. A few pollen grains of *Littorella*, and some spores of *Isoetes* and *Sphagnum* were encountered. *Scenedesmus* stays high, but in the mass of *Scenedesmus bijugatus*, *Sc. quadricauda* comes up, and *Scenedesmus costatus Schmiddle* occurs for the first time.

Gloeotrichia-like colonies are still abundant.

ATLANTICUM (Zone VII, Diagram I, IV, V)

The Atlanticum starts at the intersection of the *Pinus* and *Alnus* curves. The most striking feature of this period is the relatively low height of the *Alnus* curve, and the fact that it is surpassed by that of

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[1]) The second figure refers to the classical diagram.

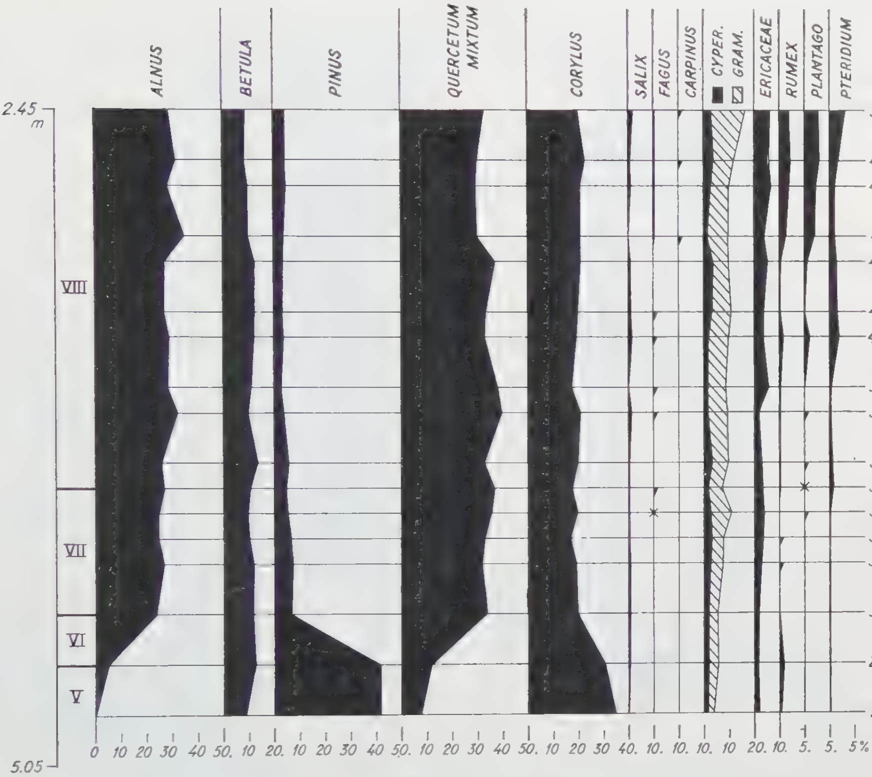


DIAGRAM IV

Classical dissolved diagrams of the Post-Glacial from the same section as in DIAGRAM I

the *Quercus* curve. In most other diagrams of the Netherlands *Alnus* is the tree which shows by far the highest value. The whole region around the "Uddeler Meer", however, was covered with dry sands; marshes and wet places which would favour aldergrowth were at a rather great distance (Fig. 1). The peats on which most Netherlands diagrams are based, were derived either from bogs grown with *Alnus* or from bogs situated near localities with a favourable environment for this species. Even in the province Drente *Alnus* regularly surpasses *Quercus*, but this area possesses much more wet places and brooks than the northern Veluwe. Our diagrams show a great resemblance to those of Jutland (IVERSEN 1941, JONASSEN 1950) and to a diagram of north-western Belgium (VANHOORNE 1951). Mrs. VERMEER-LOUMAN (1934) obtained an analogous diagram for the Wieringermeer, and HAVINGA for northern Groningen (unpublished).

Pinus stays low; its highest values are 6.6, resp. 7.8 %; its lowest at the end of the period 4.4, resp. 5.4 %; *Corylus* oscillates round 17, resp. 20 %, and shows no maximum.

Fraxinus increases and reaches a maximum of 2.7, resp. 3 %. The maximum of *Ulmus* attains 4.2, resp. 4.8 %; the curve falls to 1.6,

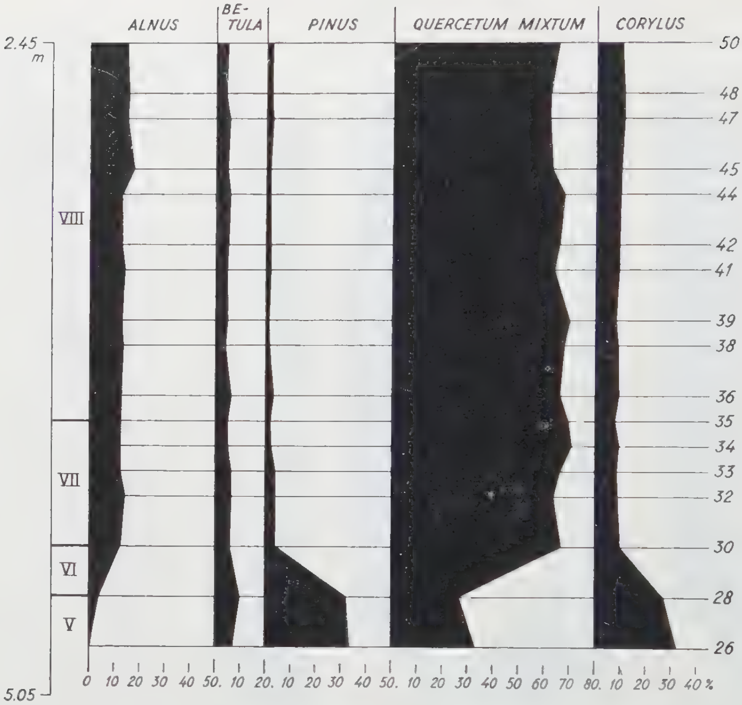


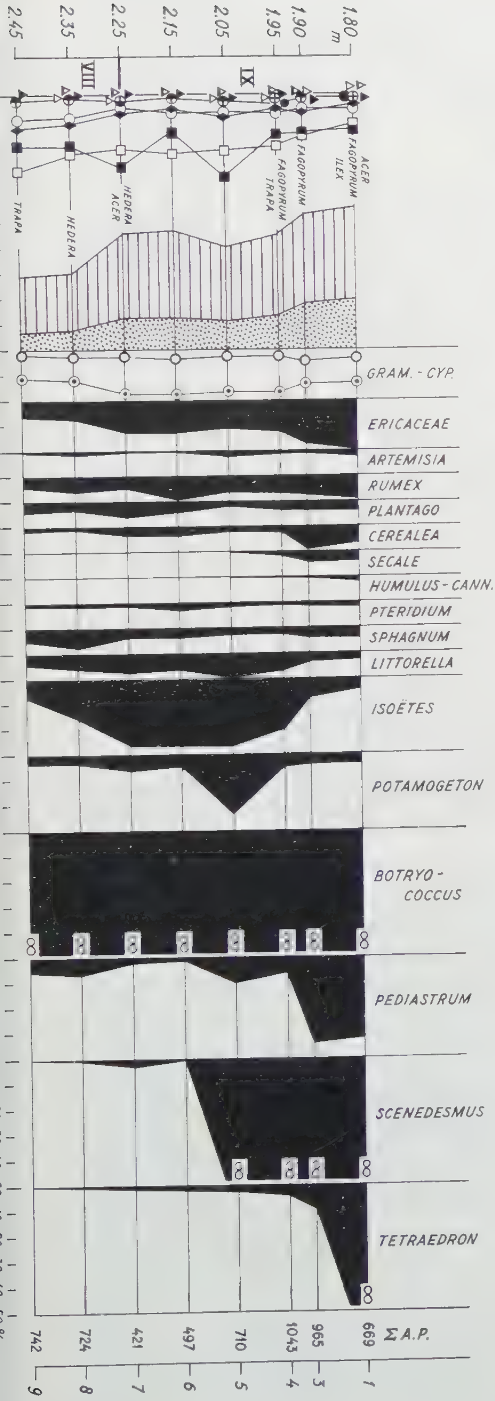
Diagram v

Dissolved and reduced diagram from the same section as in Diagram iv, to demonstrate the approximate composition of the forest in Post-Glacial times.

resp. 2 % at the close of the period. A few pollen grains of *Fagus* are found at the same time. *Picea* occurs with one or two pollen grains pro slide.

A gradual rise in N.A.P. is caused mainly by the grasses which increase from 5, resp. 6 % to 9, resp. 11 %. *Calluna* rises from 1.6, resp. 1.8 % to 3.1, resp. 3.7 %, probably on account of the leaching of the soil. *Viscum* and *Hedera* occur in a few pro mille only; *Pteridium* comes up with low values, 0.8 resp. 1 % at the close of the period. *Plantago lanceolata* was found twice; *Rumex* occurs regularly with a few pro mille, in the three last samples one pollen grain of *Hordeum* measuring 42 μ was found.

There is a distinct change in the quality of the water, which becomes oligotrophic; the sediment changes into a deep brown dy, very rich in pollen. *Nymphaea* and *Nuphar* pollen occur together with the characteristic hairs of these plants. *Potamogeton*, *Lythrum* and *Hydrocotyle* are found; towards the end of the period *Ceratophyllum* hairs become abundant. In the second half of the Atlantic period, *Isoetes* expands rapidly to a maximum of 12, resp. 14 %, *Littorella* comes up with 1.5, resp. 1.8 %. *Sphagnum* also rises, but not so much as in peat; in our deposits *Isoetes lacustre* plays the role which *Sphagnum* plays in peat.



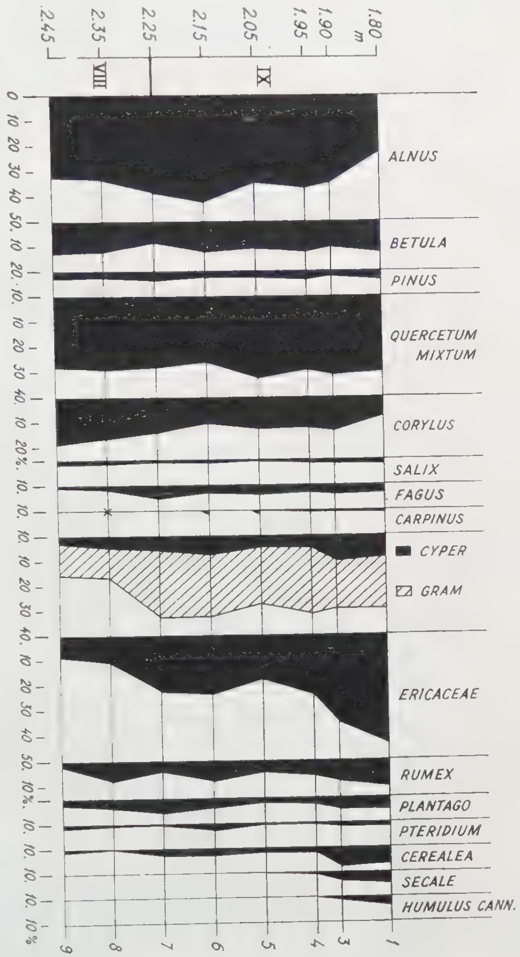


Diagram VII

Classical dissolved diagram of the same section as in Diagram VI

Diagram VI

Total diagram of the uppermost layers. Note the expansion of weeds, cereals and *Chlorophyceae*.

As to the *Algae*, *Cyanophyceae* of the *Gloeotrichia*-type disappear, but *Microchaete*-like colonies still occur. *Scenedesmus* falls to low values, and consists mainly of *Sc. costatus* with a few individuals of *Sc. quadricauda*; *Pediastrum* is low too; a new species, *P. angulosum* var. *arachnoides*, appears. *Botryococcus*, being ecologically less susceptible, shows an increase.

SUBBOREAL (Zone VIII, Diagrams I, IV, V, VI, VII)

As boundary line between the Atlanticum and the Subboreal is taken the level where the "Ulmus fall" sets in. The decline of *Ulmus*, however, is not accompanied by an increase of *Fraxinus* as it is in the Danish diagrams; but this seems to be characteristic for the Netherlands, for WATERBOLK (1954) and VAN ZEIST (1955) found the same situation.

Fagus attains a maximum of 2.9, resp. 5 %; a single pollen grain of *Carpinus* occurs. *Pinus*, *Betula*, and *Corylus* stay at the previous level.

N.A.P. rises gradually to a maximum of 46.6 % and here grasses reach the highest values with 18, resp. 33.3 %, *Ericaceae* follow with 12.6, resp. 24 % as the highest values.

As to the aquatic flora, *Isoetes* and *Littorella* increase. *Ceratophyllum* shows a decrease, followed by the *Nymphaeaceae*.

The most remarkable find is that of the characteristic pollen of *Trapa natans* in the upper half of the period; here one or two pollen grains occur regularly pro slide. Pollen of this species is only found rarely. ERDTMAN (1943) and Mme VAN CAMPO (1951) give pictures based on recent material. ASSARSON (1927) and FRIES (1951) mention *Trapa* pollen from the Atlanticum in South-Sweden and A. PRESNIKOWA (1956) reports that she has found *Trapa* pollen in gyttja from Latvia, in the warmest period, which she puts in the transition phase of the Atlanticum to the Subboreal.

Finds of *Trapa* fruits from the Post-Glacial and from the Inter-Glacial warm periods are frequent. Classical are the studies of ANDERSON (1898) and MALMSTRÖM (1920) for Finland and Sweden. The Post-Glacial fossil fruits were found far to the north of the present northern limit of the species. Those finds were considered an argument for a Post-Glacial warm period or for a continental period. *Trapa* requires summers with fairly high temperature in order to bear fruit. According to GAMS (1927) its present distribution is determined by three factors: it shuns lime, but requires much nourishment and also much heat. In North-Germany the northern limit of its area coïncides with the July isotherm of 18°. Especially the length of the period during which the water is sufficiently warm, is important for the development of fruits. According to SAMUELSSON (1934) *Trapa* reached its widest distribution in northern Europe at the end of the Litorina period, that is to say in the Bronze age. This tallies well with its occurrence in the mud of the "Uddeler Meer".

As recently as 1913, *Trapa* still grew in Lake Immeln in South Sweden. This is a typical "*Lobelia*" lake; the vegetation consists of: *Equisetum limosum*, *Isoetes lacustre* and *I. echinosporum*, *Sparganium Friesii*,

		Helianthemum		Sanguisorba						Ranunculaceae		Rosaceae		Potamogeton					Compositae								Plantago						Typha			Caryophyll.			Labiatae					
Populus	Hippophaë	oelandicum	nummularium	minor	officinalis	Epilobium	Valeriana	Cruciferae	Galium	Batrachium	Ranunculus	Geum	Potentilla	Eupotamogeton	Coleogeton	Chenopodiaceae	Urticaceae	Umbelliferae	Tubuliflorae	Liguliflorae	Lotus	Parnassia	Saxifraga oppositifolia	Oxyria	Ephedra	Nuphar	maritima	media	major	Succisa	Centaurea scabiosa	Menyanthes	sparganium ang.	latifolia	Jasione	Lychnistype	Stellaria	Scrophulariaceae	Galeopsis type	Mentha type	Botrychium	Selaginella	Sphagnum	Empetrium
	x	1		x	x	x			5				1	1	1	1	2	x			1				x	1			1	1		x	1					2				x		1
2	x		1						3			1		7	1			1	1										2			1					1			1				1
		3							1						1								1						1	1														
		8															2		5	3																2						3		

TABLE III Supplement to DIAGRAM II

		Helianthemum		Sanguisorba						Ranunculaceae		Rosaceae		Potamogeton					Compositae								Plantago						Typha			Caryophyll.			Labiatae					
Populus	Hippophaë	oelandicum	nummularium	minor	officinalis	Epilobium	Valeriana	Cruciferae	Galium	Batrachium	Ranunculus	Geum	Potentilla	Eupotamogeton	Coleogeton	Chenopodiaceae	Urticaceae	Umbelliferae	Tubuliflorae	Liguliflorae	Lotus	Parnassia	Saxifraga oppositifolia	Oxyria	Ephedra	Nuphar	maritima	media	major	Succisa	Centaurea scabiosa	Menyanthes	sparganium ang.	latifolia	Jasione	Lychnistype	Stellaria	Scrophulariaceae	Galeopsis type	Mentha type	Botrychium	Selaginella	Sphagnum	Empetrium
1		1							2			1		1				3	1					1				3	4			2	1		2				1					
	1	4	1					1	7			2	1	1				2	2					1					1	1		1	3	1		1	1	2						
	2	2		3					4		2	1		3	1			2	4					1				2	3		1									1	1	2		
		5			1		1		1			4	1	6	12	2		5											4				2								1			
		1						1	2			2		7	1		1															2	1									1		1
	1	3	4	1	1				7	1		1	2	5	6		2	4	1			1					2		1			1	1						1	2		3		1
		2							1		1	13								30																8							2	

TABLE IV Supplement to DIAGRAM III

									Polygonum				Ranunculus		Rosaceae							Compositae						Labiatae		Scrophulariaceae		Caryophyllaceae								Typha			
	Juniperus	Hippophaë	Centaura jacea	Fagopyrum	Menyanthes	Drosera rotundifolia	Myriophyllum spic.	alterniflorum	amphibium	aviculare	convolvulus	persicaria	Batrachium	Ranunculus	Geum	Potentilla	Lonicera	Thalictrum	Chenopodiaceae	Urtica	Umbelliferae	Tubuliflorae	Liguliflorae	Papillionaceae	Lotus	Solanum dulcamara	Myrica	Mentha-type	Galeopsis-type	Digitalis-type	Melampyrum	Lychnis-type	Stellaria-type	Spergula arvensis	Jasione	Campanula	Cruciferae	Succisa	Hottonia	Sparganium	latifolia	Nymphaea	Nuphar
180				1	1						x	2	4	9	4	5			7	4	5	10	11	1	1		5	2				2		2	2		2	1		18		3	1
190	1			1	1	x			x		1	1	3	6	5	5	1		5		2	10	9		3	1	6	1	4	1		1	1	5	7		6	x		3	2		
195	2	x	1	1	1	1		x		1		1	2	4	3	2			9	1	1	5	4	1	1		2	1	10	1		1	1	4	2		3	1		7	1	4	3
205									1					2		2		1	7	2	1		2				1	1	3					1	1		2	2		6			
215									2					1	1				x	1	2	2	1	1		3		4		1		2				1				2		1	
225		1							1					2	1	x			2	1			3	1	1	1	x		1	1			x			x	2	x	1	1			
235							1		x			x			2	5			1	4		4	1		2		2	1	1	2		x		1	1	x		x		4			
245									1				2	4	2	6			3	1	1	3	1						1			1			2					3			

TABLE V Supplement to DIAGRAMS VI and VII

Potamogeton natans, *Phragmites*, *Scirpus multicaulus*, *Nuphar luteum*, *Nymphaea alba*, *Myriophyllum verticillatum* and *M. alterniflorum*, *Hottonia*, *Littorella* and *Lobelia*. In the mud of the "Uddeler Meer" (Diagram I, VI, Table II, V) several of these species were found in company of *Trapa natans*.

In the Netherlands finds of *Trapa* fruits from the Post-Glacial are rare and they are not dated. In recent historic times however, *Trapa* still occurred in this country. In the Flora of de GORTER (1781) the species is mentioned for ponds and stagnant water. In 1861 OUDEMANS stated in his Flora that *Trapa* had not been found in the Netherlands since DE GORTER.

In the "Uddeler Meer" the *Trapa* pollen disappears in the Subatlanticum; but whether the species was driven away by a detoriation of the climate or by an edaphic alteration in the environment, cannot be ascertained. However, considering its present distribution, it seems likely that during the period of its occurrence the climate was more continental than nowadays. The presence of *Viscum* points in the same direction.

ALGAE

No *Cyanophyceae* of the *Gloeotrichia* type were encountered, but a few colonies of the *Gloeothece* type occurred regularly. Diatoms were scarce. *Chara* oospores, slightly differing in shape from those found in Zone I, are present.

Botryococcus is high; *Tetraedron* nearly absent; *Scenedesmus* is low, and consists mostly of the species *costata* and *quadricauda*; *Pediastrum* fluctuates.

CEREALS AND WEEDS

Since long, the "Uddeler Meer" has been an attraction object for archaeological investigations. As early as 1909, 1911 and 1912 HOLWERDA published the results of his excavations in this region. He unearthed dwelling pits and different kinds of burial sites. No megalithic graves were found, but megalithic earthenware and artefacts were met within the region. Funnel beakers, beakers with protruding foot and especially bell beakers, the latter being characteristic for the Late Neolithic of the Veluwe, occurred. It appeared that different cultures followed each other and became mixed. The bank and the surroundings of the water have been inhabited from Early Neolithic up to Carolingian times. The well known "Hunneschans" is an artificial mound erected upon natural sandridges round the lake; it enclosed a Saxon stronghold (Fig. 2).

It was the particular situation of the "Uddeler Meer" that attracted prehistoric people. According to VAN DER WAALS and GLASBERGEN (1955), in the Netherlands Neolithic remains are found especially on sand hills which formerly were bordered by extensive bogs or by low swampy regions and which usually were accessible only by way of narrow ridges. For the Beaker immigrants, accessibility, habitability, soil type and the presence of an older population, will have been determining factors. Several of these conditions were fulfilled in the vicinity of the "Uddeler Meer", which became a focus of Beaker cultures.

Human occupation is reflected in the diagrams. A gradual rise of the N.A.P. coincides with a decrease in the extent of the forest; especially the oakforest goes gradually back. However, the curves, for forest and herbs undergo some corresponding fluctuations (Diagrams I, IV, VI and VII), pronounced clearance spectra succeeded by a regeneration of the forest, as described by IVERSEN (1941, 1949), could not be established, neither is a temporary progress of birch or hazel to be seen. In sample 45, Diagram IV, however, a slight advance of alder accompanied by a retrogression in the mixed oakforest can be observed, which may have been due to a deforestation which denuded the dryer parts of the area, but left the more humid sections intact. The tendency of the alder pollen to increase at the cost of the oak pollen continues in Zone IX. This picture of forest growth on poor soil, retreating under human influence, corresponds very well with the situation depicted for western Jutland by IVERSEN (1941, 1949) and by JONASSEN (1950).

A slow rise in the N.A.P. curve, mainly caused by grasses and a gradual decrease of the Q.M., is already seen in Zone VII (Diagram I and IV). A few pollen grains of the *Hordeum* type occur in this section, together with some scattered grains of *Rumex* and *Plantago*. In Zone VIII cereals are still scarce. From a few pro mille in the lower deposit they increase slowly to a maximum of 0.7, resp. 1 % in the upper part of the section. Most pollen grains are of the *Hordeum* type; very few of the *Triticum* type are found. It proved impossible to distinguish *Triticum monococcum*, which may have been present.

HELBAEK (1952) states for southern Britain that in Neolithic and Early Bronze times *Triticum dicoccum* was the main crop on fertile calcareous soils. But "as later new and inferior areas had to be opened up to accomodate the growing population, *T. dicoccum* may have been unable to hold its own against barley, which is less susceptible ecologically". JESSEN and HELBAEK (1944) give figures with regard to the ratio of occurrence of *Triticum* and *Hordeum* in the Neolithic and Bronze Age. They conclude that in prehistoric times for long periods barley must have been the most important cereal, but that in the Neolithic Age *Triticum dicoccum* evidently equalled it. Their conclusions are based on the finding of fruits which in these selffertilising genera give still better evidence than pollen grains do.

Nevertheless it seems quite possible that in the northern part of the Veluwe *Hordeum* may have superseded *Triticum* already in the Neolithicum because of the soil conditions prevailing in this part.

In Zone VIII *Plantago*, *Rumex* and *Pteridium* increase and begin to show continuous curves. *Plantago* maxima precede those of *Rumex*, the highest values for *Plantago* being 2.4, resp. 3 %. It is most *P. lanceolata*, but there are also a few grains of *P. major*, *P. coronopus* and *P. media*. At the top of the Zone *Rumex* begins to surpass *Plantago*, attaining 2.6, resp. 8 %.

Gramineae and *Calluna* increase slowly, the *Gramineae* remaining ahead of the *Ericaceae* during the entire period. *Calluna* rises from 2.8, resp. 3.4 %, to 6.4, resp. 9 %; *Gramineae* from 8.7, resp. 10 %, to 11, resp. 16 %. Extensive fields of heather which according to VAN GIFFEN (1941) began to develop in the Subboreal, were not present in this part of the country; probably there were open spaces covered with grasses and patches of heather.

Artemisia occurs regularly with a few pro mille; *Polygonum persicaria*, *P. convolvulus*, *Sambucus* and *Rhamnus cathartica* are found too (Tables II, V).

SUBATLANTICUM (Zone IX, Diagrams VI and VII, Table V)

During this period the sediment undergoes a change; it grows thinner and thinner, and so the youngest deposits can not be sampled, the deposit flowing out of the auger. At the same time the colour lightens up; the deeper samples are still dark brown, the younger and thinner ones pale green.

The boundary line between Zone VIII and IX is not very distinct. It is placed were *Fagus* increases, *Corylus* recedes slightly, and grasses and heather expand. *Carpinus* stays very low, but begins to show a continuous curve. *Fagus* attains 2.9, resp. 5 %, Carpinus 0.4, resp. 0.9 %. The poor quality of the leached sands prevents the expansion of those trees, and may also be the cause that *Corylus* maxima are lacking in our diagrams. *Myrica* is very scarce, only a few pro mile.

N.A.P. increases to 55.4 %. *Alnus* expands, and sometimes surpasses or equals the mixed oak forest, in which *Quercus* predominates very strongly; *Tilia* and *Ulmus* fall down to a few pro mille only.

AQUATIC VASCULAR PLANTS AND ALGAE

In this period *Trapa natans* disappears. Next to a change in the climate it seems likely that a change in the chemical composition of the water may have been responsible. *Potamogeton* expands; high values for pollen are found together with several fruits. Some could be identified as *P. obtusifolius*, *P. acutifolius* and *P. natans*, JESSEN (1955). *Littorella* and *Isoetes* recide (Diagram VI); *Ceratophyllum* and *Nymphaeaceae* are still present; according to IVERSEN (1929), they occur in all types of water.

It looks as if the water becomes eutrophic. The green *Algae*, *Scenedesmus*, *Pediastrum* and *Tetraedron* show a considerable rise, and reach very high values in the uppermost deposits. The bulk consists of *Scenedesmus* among which *S. bijugatus* is the main component, but *S. costatus* and *S. quadricauda* occur too. The pale green colour of those upper deposits is mainly caused by *Scenedesmus*. Among the *Tetraedron* species *T. muticum* predominates, but a new species comes up, viz. *T. caudata*. *Pediastrum boryanum*, *P. duplex f. subgranulatum* and *P. angulosum* occur too, the first species being most abundant. The dark brown dy gradually changes into a gyttja in *statu nascendi*. This coincides with the cultivation of rye and with the expansion of the fields of heather; i.e. with the time when human occupation is at its peak.

Owing to the deforestation the content of sand in the deposit increases. It seems highly probable that the water became eutrophic because of man and his refuse.

CEREALS AND WEEDS

During the Subatlanticum the cereals continue to increase slowly. *Hordeum* is still the main component, but some *Triticum* occurs too. In sample 5 at 2.05 m under the surface *Secale* makes its appearance with two grains. The values for cereals are then 1, resp. 2 %, *Secale* included. According to MIKKELSEN (1954), the first appearance of *Secale* coincides with the Roman Iron period, RY II. At the same time a slight regeneration of the forest and a recession in the N.A.P. may be observed (Diagram VI and VII). Archeological finds are rare in this period; this together with the behaviour of the vegetation might lead to the conclusion, that the region was more or less abandoned in the Roman Iron time. MIKKELSEN (1954) supposes that this period was warmer and drier than the previous one, so that the cultivation of dry soils declined, and the more fertile humid areas became arable, which caused a migration of the inhabitants. MODDERMAN (1955) states that in the first two centuries of our era, the Betuwe (south of the Veluwe, a silt-covered region between the branches of the river Rhine) became densely inhabited. In that time the water level fell, and the higher parts, i.e. the sand ridges and river banks, became habitable. In the first half of the third century many dwelling places were abandoned because of the greater humidity of the climate and the rising water level, a situation which favoured the drier soils. Could it be that there was a migration from North to South and vice versa?

While *Hordeum* and *Triticum* maintain the same level, *Secale* at first rises slowly and more quickly in the upper samples. Cereals, *Secale* included, reach maxima of 5, resp. 7 %. *Centaurea cyanus* does not occur in our samples. According to MIKKELSEN (1954, 1955) this species did not appear in rye fields before about 1300; its arrival probably coincided with the introduction of wintercorn. In the upper three samples a single pollen grain of *Fagopyrum* is found. Buckwheat, was recorded by VAN ZEIST in the Bronze Age (in VAN GIFFEN 1954), by MIKKELSEN at the close of Iron Age on Bornholm (1954). In the same year DIECK published a study on the history of buckwheat in which he states that in the Middle Ages *Fagopyrum* has been imported from Eastern Europe. In 1396 it was mentioned for the first time in the archives of Nürnberg.

It seems that in our case *Fagopyrum* occurred at the close of the Iron Age, before *Centaurea cyanus* appeared in the rye fields.

Together with cereals, there is a pronounced rise in the values for weeds. *Rumex* surpasses *Plantago* and attains maxima of 5, resp. 11 %, *Plantago* 2, resp. 4.6 %. According to WATERBOLK (1958) this might indicate a change from cattle breeding and grazing to agriculture. *Spergula* occurs regularly; *Polygonium persicaria*, *P. convolvulus* and *P. aviculare* are present. A new element is the pollen either of *Humulus* or *Cannabis*, which appears in the form of a regular curve with maxima of 1, resp. 3 %.

During the Subatlanticum the *Ericaceae* rise sharply from 6.4, resp. 9 % to 19.6, resp. 44 % in the uppermost sample. In this section they surpass the grasses, which rise from 11, resp. 16 %, to 13.5, resp. 30 %. For *Calluna* no percentages of over 100 are met with. The very high values for *Ericaceae* in many Netherlands diagrams, however, are from peat, where local influence is considerable (Brouwer, 1947, Van Zinderen Bakker, 1948, Van Zeist, 1955). We could not continue our sampling up to younger historic times and had to stop at approximately the early Middle Ages. It is supposed that the very great expansion of the fields of heather took place at the beginning of the nineteenth century (Jonassen, 1935, 1950).

At the time of our upper samples the landscape showed oak forest, heath, cultivated fields and grassy plains, maybe heather interspersed with grasses. This picture of the region is in good agreement with Edelman's interpretation of the name "Veluwe" (1958, 1959). He points out that "Betuwe" and "Veluwe" are names often heard at old dwelling places, and that they apply to grass fields on former forest soil. "Veluwe" to this sense means "yellow meadow", in contrast to heath or to green grass fields. As grasses on sandy soils after flowering soon turn yellow, the landscape will have had this colour during most of the year.

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SUMMARY

The diagrams of the "Uddeler Meer" cover the history of the vegetation from Late-Glacial (Dryas I) to early historic times. All the analyses have been made from organic sediment (mud).

Late-Glacial

The zonation of Jessen and Iversen (Faegri and Iversen, 1950) is used. In Zone I (Older Dryas time) no Bølling oscillation could be detected. *Juniperus* attains high values (over 20 %), *Artemisia* 5 %.

Zone II (Allerød) is characterised by a *Pinus* maximum in the upper section. At that time *Pinus* forests must have occurred near the bank, as *Pinus* stomata are found in the samples.

In Zone III (Younger Dryastime) *Juniperus* stays low, *Artemisia* increases, *Empetrum* attains a maximum of 3.9 %, and *Dryopteris linnaeana* shows a continuous curve (maximum 12 %).

The sediments of Zone I and III are greyish green in colour; the Allerød sediments (Zone II) are olive. The deposits of Zone I are rich in lime.

Post–Glacial

ZONE IV (Preboreal) is hardly developed.

ZONES V and VI (Boreal), with maxima of *Pinus* and *Corylus*. Again stomata of *Pinus* are found; only in Zone II and V *Pinus* was important. After Zone VI *Corylus* has no more maxima.

ZONE VII (Atlanticum). In this section the most remarkable feature is that *Quercus* predominates over *Alnus*, as this is quite exceptional in the Netherlands. *Viscum* and *Hedera* occur in a few pro mille only.

ZONE VIII (Subboreal). After the *Ulmus* fall, *Fagus* begins to show a continous curve with low values. *Fraxinus* fluctuates between 2 and 3 %, but shows no distinct maximum.

ZONE IX (Subatlanticum). *Carpinus* stays under 1 %, and of *Myrica* only scattered pollen grains were found in the youngest deposits. In the last samples some pollen grains of *Juniperus* and *Hippophaë* were met with.

Cereals and Weeds

Traces of cereals and weeds occur already in the Atlanticum, in the Subboreal however they become numerous. Among the cereals *Hordeum* predominates, *Triticum* is scarce; together they attain a maximum of 1 %. In the Subatlanticum cereals rise, mainly due to the arrival of *Secale*; the first pollen grains appear towards the middle of this section. In the uppermost samples *Fagopyrum* occurs, *Secale* rises to 4.3 % and the other cereals to 2.8 %.

The N.A.P. curve rises gradually, but shows a rapid increase in the Subatlanticum. The main components are grasses and *Ericaceae*; the *Gramineae* surpass the *Ericaceae* till the point is reached where *Secale* begins to expand. At the end of the Subboreal the *Ericaceae* attain 23 %, in the Subatlanticum 44 %. The final expansion of *Calluna* must have taken place in late historic times.

Plantago, *Rumex* and *Pteridium* begin to show continuous curves in the Subboreal. At first *Plantago* surpasses *Rumex*; in the Subatlanticum *Rumex* (maximum 11 %) exceeds *Plantago* (maximum 4.6 %). *Polygonum persicaria*, *P. convolvulus* and *P. aviculare* occur. In the younger samples *Spergula* appears; a kind of pollen which may be either *Humulus* or *Cannabis* shows a continuous curve.

Aquatic flora

The "Uddeler Meer" started as a hard water pond, rich in *Characeae*. In the Older Dryas time *Chlorophyceae* and *Cyanophyceae* were present to such an extent that they gave colour to the sediment.

Pediastrum, *Scenedesmus*, *Tetraedron* and *Botryococcus* have been counted.

Tetraedron has a peak in Zone I, and decreases rapidly in Zone II, but in the Subatlanticum it reappears with high values.

Scenedesmus stays high up to the Atlanticum; thereafter it falls to low values, and reappears in very great numbers in the Subatlanticum.

Pediastrum is very high in the Late-Glacial, especially in Zone I. During the Post-Glacial it fluctuates around rather high values, and increases strongly in the upper Subatlanticum.

Botryococcus is high throughout the entire series; it increases still further towards the end.

Cyanophyceae occurred especially in the Late-Glacial; they could not be identified with certainty, and have not been counted.

As to the aquatic Vascular Plants, *Littorella* and *Isoetes* show continuous curves in the Atlanticum with relatively high values.

The most remarkable find is that of *Trapa natans* pollen in the upper section of the Subboreal; it is represented there by one or two grains pro slide. It vanishes in the Subatlanticum.

REFERENCES

ANDERSON, GUNNAR. 1898. Bull. Géol. de Finlande. **8**: 1.
– ———. 1927, Geol. Fören. Förh. **49**: 293.

BROUWER, AART. 1947. Tijdschr. Kon. Ned. Aardr. Gen. **64**: 1.

CAMPO, M. VAN. 1951. Bull. Soc. Bot. du Nord de la France. **4**: 36.

EDELMAN, C. H. 1958. Bijlagen en Meded. der Naamk. Comm. v.d. Kon. Ak. v. Wet. Amsterdam. **12**: 1.

———. and A. W. EDELMAN–VLAM. 1959. Boor en Spade **10**: 74.

ERDTMAN, G. 1943. An Introduction to Pollenanalysis. Waltham, Mass.

FAEGRI, KNUT. 1939–1940. Bergens Mus. Arsb. Naturv. Rekke. **7**: 1.

FLORSCHÜTZ, F. und E. C. WASSINK. 1941. Rec. Trav. Bot. Néerl. **38**: 1.

FRIES, MAGNUS. 1951. Acta Phytogeogr. Suecica. **29**: 1.

GAMS, H. 1927. Die Pflanzenareale. **1**: 39.

GIFFEN, A. E. VAN. 1954. Uitg. Ned. Heidemij. Arnhem. 78.

———. 1954. Gelre. **4**: 54.

GODWIN, H. 1956. The History of the British Flora. Cambridge.

GORTER, D. DE. 1781. Flora Provinciarum Belgii Foederati. **7**: Haarlem.

GROHNE, UDELGARD. 1957. Photographie u. Forschung. **7**: 237.

GÖTTLICH, K. H. 1955. Beitr. z. naturk. Forschung in S. W. Deutschland. **14**: 88.

HAMMEN, TH VAN DER. 1950. Leidse Geol. Meded. **17**: 1.

HEDBERG, O. 1946. Svensk Bot. Tidskrift. **40**: 371.

HELBAEK, H. 1953. Prehistoric Society. **18**: 194.

———. 1953. Ann. Rep. Inst. Archaeol. London 44.

HOLWERDA, J. H. 1909. Oudh. Meded. v.h. Rijksmuseum v. Oudheden te Leiden. **3**: 1.

———. 1911. Oudh. Meded. v.h. Rijksmuseum v. Oudheden te Leiden. **5**: 5.

———. 1912. Oudh. Meded. v.h. Rijksmuseum v. Oudheden te Leiden. **6**: 1.

IVERSEN, J. 1929. Bot. Tidskrift. **40**: 277.

IVERSEN, JOHS. 1941. Danm. Geol. Unders. II Ser. **66**: 1.

———. 1949. Danm. Geol. Unders. IV Ser. **13**: 5.

———. 1951. Medd. Dansk Geol. For. **12**: 174.

———. 1954. Danm. Geol. Unders. II Ser. **80**: 73.

JESSEN, KNUD and HANS HELBAEK. 1944. D. Kon. Danske Vidensk. Selsk. **3**: 1.

JESSEN, K. 1955. Dansk Bot. Tidskr. **52**: 1.

JONASSEN, H. 1935. Bot. Tidskrift. **43**: 187.

———. 1950. Dansk Bot. Arkiv. **13**: 5.

LANG, GERHARD. 1952. Flora. **139**: 243.

———. 1952. Beiträge z. naturk. Forschung in S.W. Deutschland. **9**: 89.

LORIE, J. 1910. Verh. Kon. Ak. v. Wet. Amsterdam. 2e Sectie. **16**: 36.

MAARLEVELD, G. C. and J. C. VAN DER TOORN. 1955. Tijdschr. Kon. Ned. Aardr. Gen. **72**: 344.

MALMSTRÖM, CARL. 1920. Svensk Bot. Tidskrift. **14**: 1.

MIKKELSEN, VALDEMAR. 1948–1950. Dansk Bot. Arkiv. **13**: 7.

———. 1954. Danm. Geol. Unders. II Ser. **80**: 210.

MODDERMAN, P. J. R. 1955. Tijdschr. Kon. Ned. Aardr. Gen. **72**: 30.

OUDEMANS, C. A. J. A. 1861. De Flora van Nederland ten behoeve van het algemeen beschreven. Haarlem. **2**.

PRESNIKOVA, A. 1956. Latv. P.S.R. Zinat. AK. Vest. **1**: 53.

SAMUELSSON, GUNNAR. 1934. Phytogeographica suecica. **4**: 1.

STRAKA, HERBERT. 1952. Arb. zur Rheinischen Landesk. **1**: 1.

———. 1954. Flora. **141**: 101.

———. 1954. Congrès int. de Bot. Paris. **7**: 242.

———. 1958. Flora. **146**: 412.

TERASMAË, J. 1951. Svensk Bot. Tidskr. **45**: 358.

VANHOORNE, ROGER. 1951. Bull. Inst. Royal des Sc. nat. de Belgique. **27**: 1.

VERMEER–LOUMAN, G. 1934. Pollenanalytisch Onderzoek van den West-Nederlandschen Bodem. Thesis. Amsterdam.

WAALS, J. D. VAN DER and W. GLASBERGEN. 1955. Palaeohistoria. **4**: 5.

WATERBOLK, H. T. 1955. De praehistorische mens en zijn milieu. Assen.

———. 1958. Palaeohistoria **5**: 39.

WODEHOUSE, R. P. 1935. Pollengrains. New York and London.

ZAGWIJN, W. H. 1952. Geologie en Mijnbouw. **14**: 1.

ZEIST, W. VAN. 1955. Acta Bot. Neerlandica. **4**: 1.

ZINDEREN BAKKER, E. VAN. 1948. Tijdschr. Kon. Ned. Aardr. Gen. **55**: 174.

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